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BULLETIN OF
THE BRITISH MUSEUM
(NATURAL HISTORY)

BRITISH MUSEUM
11 SEP 1970
NATURAL HISTORY

GEOLOGY
VOL. XVII
1968–1969

TRUSTEES OF
THE BRITISH MUSEUM (NATURAL HISTORY)
LONDON: 1970

DATES OF PUBLICATION OF THE PARTS

No. 1. 19th November 1968
No. 2. 19th November 1968
No. 3. 17th January 1969
No. 4. 17th January 1969
No. 5. 21st January 1969
No. 6. 7th March 1969
No. 7. 15th April 1969
No. 8. 16th May 1969

PRINTED IN GREAT BRITAIN
BY ALDEN & MOWBRAY LTD
AT THE ALDEN PRESS, OXFORD

CONTENTS

GEOLOGY VOLUME XVII

No. 1. On the Cretaceous age of the so-called Jurassic Cheilostomatus Polyzoa (Bryozoa). A contribution to the knowledge of the polyzoa-fauna of the Maastrichtian in the Cotentin (Manche). E. VOIGT 1

No. 2. The caudal skeleton in Mesozoic Acanthopterygian fishes. C. PATTERSON 47

No. 3. Non-calcareous microplankton from the Cenomanian of England, Northern France and North America. Part I : R. J. DAVEY 103

No. 4. A redescription of W. Carruthers ' type Graptolites. I. STRACHAN 181

No. 5. A revision of the English Wealden Flora, I Charales-Ginkgoales. J. WATSON 207

No. 6. Two new Dicynodonts from the Triassic Ntawere Formation, Zambia. C. B. COX 255

No. 7. Lower Cambrian Archaeocyatha from the Ajax Mine, Beltana, South Australia. F. DEBRENNE 295

No. 8. Some Bathonian Ostracoda of England with a revision of the Jones 1884, and Jones & Sherborn 1888 Collections. R. H. BATE 377

Index to Volume XVII 439

ON THE CRETACEOUS AGE OF THE SO-CALLED JURASSIC CHEILOSTOMATUS POLYZOA (BRYOZOA)

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BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
GEOLOGY Vol. 17 No. 1
LONDON : 1968

BRITISH MUSEUM
18 NOV 1968
NATURAL HISTORY

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BY

EHRHARD VOIGT

Pp. 1–45; 8 *Plates*; 2 *Text-figures*

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THE BULLETIN OF THE BRITISH MUSEUM (NATURAL HISTORY), *instituted in* 1949, *is issued in five series corresponding to the Departments of the Museum, and an Historical series.*

Parts will appear at irregular intervals as they become ready. Volumes will contain about three or four hundred pages, and will not necessarily be completed within one calendar year.

In 1965 *a separate supplementary series of longer papers was instituted, numbered serially for each Department.*

This paper is Vol. 17, *No.* 1 *of the Geological Palaeontological series. The abbreviated titles of the periodicals cited follow those of the World List of Scientific Periodicals.*

World List abbreviation
Bull. Br. Mus. nat. Hist. (Geol.).

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TRUSTEES OF
THE BRITISH MUSEUM (NATURAL HISTORY)

Issued 19 *November* 1968

Price £2

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By EHRHARD VOIGT

SYNOPSIS

The supposed Jurassic cheilostomatous Polyzoa described by J. W. Gregory (1894) as *Membranipora jurassica* and *Onychocella bathonica* from the Bathonian of Ranville (Calvados), are of Cretaceous age and must have come from the Maastrichtian of the Cotentin (Manche, France). The matrices of the type specimens yielded thirty-three further species of Maastrichtian Polyzoa of which nine are Cyclostomata and twenty-four Cheilostomata. Three new species *Radulopora minor* n. sp., *Rosseliana thomasi* n. sp. and *Frurionella fertilis* n. sp., and the new genus *Radulopora* are described.

CONTENTS

I. INTRODUCTION AND ACKNOWLEDGMENTS 3
II. CHEILOSTOMATA OF CRETACEOUS AGE DESCRIBED FROM JURASSIC BEDS 4
III. POLYZOA FROM JURASSIC BEDS WHICH HAVE BEEN ERRONEOUSLY REFERRED TO THE CHEILOSTOMATA 9
IV. ON THE ORIGIN OF GREGORY'S " JURASSIC " CHEILOSTOMATA . . 10
V. PALAEOZOIC CHEILOSTOMATA? 13
VI. THE ACCOMPANYING FAUNA OF THE ROCK-MATRIX OF GREGORY'S " JURASSIC " CHEILOSTOMATA 14
VII. REFERENCES 42

I. INTRODUCTION AND ACKNOWLEDGMENTS

THE predominant orders of Polyzoa (Bryozoa) of the Cretaceous and Cainozoic periods are the Cyclostomata and the Cheilostomata. The Cheilostomata have been increasing ever since an explosive development in the Upper Cretaceous, whereas the Cyclostomata have decreased during the Tertiary and Quaternary following a flourishing period in the Cretaceous. Today there exists only a comparatively small relic of this cyclostomatous fauna stem which, in Jurassic times, was the only living group of Polyzoa apart from some rare species of boring Ctenostomata.

This last statement contradicts all textbooks of palaeontology in which the Cheilostomata are being erroneously recorded as beginning at the latest in the Jurassic, an opinion repeated by R. S. Bassler (1953).

It is the purpose of this paper to prove that the so-called Jurassic Cheilostomata described by Gregory (1894) from the Bathonian of Ranville (Calvados), are in fact

Upper Cretaceous in age and must have their origin in the Maastrichtian of the Cotentin (Manche) in Normandy.

Other Jurassic Polyzoa described as Cheilostomata by several authors do not belong to that order but are true Cyclostomata. In any case it must be emphasized that, if they are undoubtedly Jurassic, they are not Cheilostomata, or if they belong to that order they are not Jurassic.

I wish to record my warm appreciation of the late Dr. Dighton Thomas of the British Museum (Natural History) to whom I am very much indebted for studies in the Museum collection, for the loan of specimens, for discussion, and for his help and advice. At the time of his death he had begun tidying the English of the manuscript, and this was kindly finished by Dr. J. M. Hancock. I am also grateful to Dr. A. B. Hastings for interesting discussions about the subject. Grateful thanks are due to Prof. J. Lehman, Dr. J. Sornay and Dr. E. Buge of the Musée d'Histoire Naturelle (Paris) for permission to study and to photograph the types of Bryozoa in the d'Orbigny-Collection. I also wish to thank Dr. J. Roger, Paris, for kindly accompanying me and guiding me in the Maastrichtian territory of the Cotentin and other French classic localities. Finally my special thanks are due to the Deutsche Forschungsgemeinschaft for financial help to further this research and their support for my studies on Cretaceous Polyzoa.

II. CHEILOSTOMATA OF CRETACEOUS AGE DESCRIBED FROM JURASSIC BEDS

Considering first the ages of undoubted Cheilostomata which have been described as Jurassic forms, we can enumerate the following three species: *Flustra flabelliformis* Lamouroux 1821, *Onychocella bathonica* Gregory 1894, and *Membranipora jurassica* Gregory 1894.

1. "***Flustra***" ***flabelliformis*** Lamouroux 1821

1821 *Flustra flabelliformis* Lamouroux: 113, pl. 76, figs. 11–13.

This species, described in a footnote and figured by Lamouroux, apparently from Ranville, is a fanlike fragment of a bilaminar *Onychocella*. The very simple figure shows pyriform zooecia with round orifices increasing in size to the periphery of the frond. An avicularium, rounded distally, seems to be indicated. Below the broken cryptocyst the rectangular or box-like pattern of the zooecia is visible. The original diagnosis of Lamouroux is:

> "*Flustra* en forme d'éventail, fossile, épaisse, à bords entiers, composée de deux membranes, une supérieure mince, un peu translucide, divisée en alvéoles profonds, à bords irréguliers avec un oscule rond dans le centre, qui communique à une cellule en forme de carré long, très regulier, avec des cloisons épaisses et solides, les transversales alternant entre elles, les longitudinales se prolongeant sans interruption de la base aux extrémités; grandeur, 2 à 3 centimètres; épaisseur, environ 1 millimètre."

Unfortunately there is no possibility of restudying the typespecimen because, according to Sherborn, Lamouroux's collection has been lost. Nevertheless, there is no doubt that the specimen is not from the Bathonian of Ranville as supposed by Gregory, but must be regarded as a Cretaceous *Onychocella*, likely to have come from one of the Maastrichtian localities of the Cotentin (Manche), as is demonstrated for the two following species. Lamouroux himself gives as the origin only the neighbourhood of Caen, which perhaps includes not only Ranville but also the Cotentin.

Gregory (1896 : 214) in his Catalogue of the Jurassic Bryozoa in the British Museum suppressed his specific name *bathonica* for an *Onychocella*, regarded by him in 1894 as a new species from the Bathonian of Ranville, in favour of Lamouroux's species because he believed that the two forms were identical.

As will be shown, Gregory's *Onychocella bathonica* is the well-known Maastrichtian *Onychocella piriformis* Goldfuss 1826 first described from the " Maastrichter Tuffkreide " in the Netherlands. If Gregory was correct in identifying his *Onychocella bathonica* with *Flustra flabelliformis* Lamouroux, the latter name has priority. On the other hand Lamouroux's figure is rather unsatisfactory, as Gregory himself stated, for a conclusive identification of *Flustra flabelliformis* Lamouroux with *Onychocella piriformis* Goldfuss. There are so many similar species of *Onychocella* in the Upper Cretaceous that it seems to be quite impossible to find out which species was intended by Lamouroux under this name. Gregory notes that Lamouroux's figure is so indefinite that Pictet gave a figure of a form, which he referred to this species, which was really *Diastopora lamellosa* Michelin. It is probable that Gregory, in identifying his *Onychocella bathonica* with Flustra *flabelliformis*, was influenced by his supposition that they are of Bathonian age, and as Jurassic species of *Onychocella* must be very scarce, he believed that they must be identical.

2. " **Onychocella bathonica** " Gregory 1894
(= *Onychocella piriformis* Goldfuss 1826)

(Pl. 5, figs. 11–12)

1826 *Eschara piriformis* Goldfuss: 23, pl. 8, fig. 10.
1851 *Eschara piriformis* (Goldfuss) von Hagenow: 75, pl. 9, fig. 6 and pl. 11, fig. 6.
1894 *Onychocella bathonica* Gregory : 63, fig. 2
1896 *Onychocella flabelliformis* (Lamouroux) ; Gregory : 214, fig. 22.
1930 *Onychocella piriformis* (Goldfuss); Voigt: 454, pl. 16, figs. 1–2.

This is the supposed Jurassic cheilostomate which was described and figured by Gregory under this name in 1894 and, as stated above, later treated by him as a synonym of " *Flustra* " *flabelliformis* Lamouroux. The first mention of a " Jurassic *Onychocella* " was made by Gregory (1893 : 239). It is represented in the British Museum Collection by two specimens, D.181 (type) and D.480, both from the Tesson-Collection. As previously suggested by the present author (Voigt 1930 : 454), these two specimens are not from the Bathonian " Calcaire à polypiers " as recorded by Gregory, but both are Upper Cretaceous in age. This is proved firstly by a Cheilostomatous Polyzoan, *Stamenocella marginata* (d'Orbigny) which is visible in the matrix of specimen D.181 (Pl. 3, fig. 1) and which was overlooked by Gregory, and secondly by a large fauna of other Maastrichtian Polyzoa which has been isolated from the adherent matrix of the block D.181 and which is described in section VI. This study shows clearly that all these supposed Bathonian Polyzoa are in fact of Upper Cretaceous age as already indicated for "*Membranipora jurassica*" by Lang (1916 : 96, 97 and 1922 : 197–198) and Larwood (1962 : 223).

Onychocella bathonica Gregory is the same species as *Onychocella piriformis* (Goldfuss) 1826 from Maastricht. It is quite commonly found in various localities of the French Cotentin (Manche). Although Gregory has discussed Goldfuss's species and written that it has a lower zooecial aperture, while the avicularian aperture is larger and the front wall occurs only above and not on both sides of this, a comparison with a specimen from Chef du Pont indicates that they are synonyms (pl. 5, fig. 11). The supposed differences are not significant and they are not found when material from Maastricht or from the Cotentin localities is used for comparison. Some of the opesiae[1] in the figured (pl. 5, fig. 12) British Museum specimen D.181 are a little smaller than those of the figured specimen from Chef du Pont (pl. 5, fig. 11), but there are variations within the same specimen. Gregory's figure is deceptive because it shows a small quadrangular fragment with only five whole zooecia and one avicularium; it does not correspond in size to his two originals. The Holotype of *Onychocella bathonica* Gregory is a large bent unilaminar frond of nearly 3 cm. length (pl. 5, fig. 12). It contains a dozen avicularia and shows, on some zooecia, the very small characteristic endozooecial ovicells which are just visible as minute swellings at the distal ends of the zooecia figured here (pl. 5, fig. 12). The other specimen D.480 is a large unilaminar fragment of 11 × 8·5 cm. size with four avicularia.

In discussing the affinities of *Onychocella flabelliformis* (Lamouroux) Gregory maintains that its nearest ally may be von Hagenow's *Cellepora* (*Discopora*) *koninckiana* (1851 : 95, pl. 11, figs. 11–12) from Maastricht, a species which, with its straight rows of avicularia and small zooecia, is very differently shaped. In discussing *Onychocella* (= *Cellepora*) *koninckiana* (1896 : 215) he distinguished the form figured by von Hagenow in his fig. 11 as a new species—*Onychocella hagenowi*. He assigned it to a separate species because he believed that it has larger elliptical opesiae with the longer axis longitudinal, an entire lower margin of the opesia and much larger avicularia. This example shows how dangerous it is to judge the variability of species on the evidence of figures alone. Von Hagenow was quite correct in considering the two forms as only one species because they can often be observed in the same zoarium as confirmed by Voigt (1930 : 460).

The first known species of *Onychocella* are from the Cenomanian, and they are small and of a lower level of evolution. Judging from this point of view it would be very odd if the oldest species should have the largest zooecia of the genus, more than 1 mm. long, and big avicularia 1·3–1·4 mm. in length as these are otherwise developed only at the acme of the Onychocellids in the late Upper Cretaceous.

---

[1] I have followed the advice of Dr. Hastings in using "opesia", plural "opesiae", rather than "opesium", plural "opesia".

3. *Castanopora jurassica* (Gregory) 1894

(Pl. 7, figs. 4–7)

1894 *Membranipora jurassica* Gregory: 62, text-fig. 1.
1896 *Membranipora jurassica* Gregory: 212, text-fig. 21, p. 213.
1916 *Rhiniopora jurassica* (Gregory) Lang: 96.
1922 *Rhiniopora scabra* Lang: 196, pl. 4, fig. 7, text-fig. 62.
1922 *Rhiniopora jurassica* (Gregory) Lang: 197.
1962 *Castanopora jurassica* (Gregory) Larwood: 223, pl. 17, figs. 3–5, text-figs. 108–109.

Holotype D.180, large bilaminar fragment of damaged zoarium partly embedded in matrix. Upper Maastrichtian, Cotentin, Manche, France (not Maastricht, Netherlands).

Lang recognized the cribrimorph nature of this species. It was overlooked by Gregory that the cribrimorph structure of the frontal-shield was preserved quite well in some zooecia of the type specimen D.180 (Tesson Coll.) which was figured by Larwood (1962 : 224, text-fig. 108, pl. 17, fig. 5). Although Gregory described it correctly as " erect foliaceous, bilaminate ", Lang defined this form as " encrusting unilaminar " as did Larwood (1962). Dr. Dighton Thomas and Dr. A. Hastings were kind enough to confirm my first observation made in the Museum collection that Gregory's type specimen is bilaminar and not encrusting.

Gregory, misled by the erroneous data of Tesson's label, recorded the species as coming from the Bathonian of Calvados. Lang (1922 : 197) recognizing the Maastrichtian age, supposed that it originated from the Dutch locality Maastricht itself, and recorded the distribution of this species as, " Senonian, Maastrichtian, Maastricht, Limburg, Holland ", specimen D.3313 being labelled " Maastricht, Old collection ". Larwood (1962, pl. 17, fig. 3) followed Lang and gave a photograph of this specimen. I am much indebted to Dr. Dighton Thomas for lending me D.3313, for there is no other record of *Castanopora jurassica* from Maastricht, and the specimen may have come from the same locality as D.180. Dr. Dighton Thomas compared the matrices of these two specimens: they are very similar in colour, grain size, and in size of fossil debris, and they could have come from the same locality in the Cotentin.

As will be shown in section IV of this paper, the type locality cannot be Maastricht in Holland, but must be the same as that of the last species, a locality in the Cotentin. The matrix of the type specimen D.180 is a hard, Polyzoan-bearing, detrital limestone, resembling very much the " Craie à Baculites " or " Craie à Thécidées " of the Cotentin. Lang has already recognized some other Cheilostomata in the matrix of this block. They are described and figured here under the name of *Multicrescis laxata* d'Orbigny, *Rosseliana thomasi* n. sp. and *Pliophloea* sp. These species are unknown from Maastricht itself, and combined with the results above on " *Onychocella bathonica*", there can be no doubt that the two species both come from the Cotentin.

All this is now confirmed by the fact that I have found four fragments of " *Castanopora* " *jurassica* (Gregory) in my material from Chef du Pont (Cotentin, Manche).

Dr. Dighton Thomas kindly compared them with the holotype, and he has no doubt that they represent the same species. They agree in measurements, in number of costae, and all other characteristics. All are bilaminar with the exception of a young zoarium which is unilaminar and whose zooecia are only 0·09–1·00 mm. long. In the others the very large zooecia are about 1·2–1·4 mm. long. There are about twenty-six to thirty-four costae with eight lateral costal fusions as stated by Larwood. Pl. 7, fig. 5 shows an instructive view with some zooecia, one of which has preserved its undamaged cribrimorph front wall; the others are broken and show the " membranimorph " habit of Gregory's figure. On the reverse side of the specimen (Pl. 7, fig. 4) are some zooecia with the characteristic ovicells of the genus which were previously not known in full preservation. They are hyperstomial and globular, prominent, and overlapping the distal zooecium as presumed by Larwood. They are perforated by isolated fine pores (invisible in my figure) as in *Castanopora guascoi* Ubaghs from Maastricht.

It must be emphasized that *Castanopora jurassica* (Gregory) has never been found near Maastricht, although I have studied the Polyzoa of the Maastrichtian Tuffkreide for 40 years. Near Maastricht another allied bilaminar form is represented, *Castanopora guascoi* (Ubaghs) (1865 : 51, pl. 2, fig. 3), whose zooecia in some cases reach a length of 1·5 mm. but which has fewer costae (fifteen to twenty-two). Specimens like these were described by von Hagenow as *Cellepora* (*Dermatopora*) *faujasi* (von Hagenow : 1851, p. 99, pl. 10, fig. 19). It is impossible to mistake *Castanopora guascoi* for *Castanopora jurassica* (Gregory), but it is of interest that, if the costae are broken down, this species gives the appearance of *Membranipora bipunctata* (Goldfuss 1826 : 26, pl. 9, figs. 7a–b), traces of costae being no longer visible. The Cotentin fauna contains further allied bilaminar and unilaminar species which could be mistaken for *Castanopora jurassica*, but there is little room to discuss them. *Rhiniopora scabra* Lang 1916 from Rügen is, according to Larwood, a synonym of *Castanopora jurassica* Gregory, because it agrees in general with the number of costae, and in having 8 lateral costal fusions and pelmatidia.

In a recent work (Voigt 1968 : 65) finished before the issue of the present paper, the genus *Rhiniopora* Lang 1916, united with *Castanopora* by Larwood (1962), is maintained at least as a subgenus of *Castanopora*.

SPECIMENS:

D.3313. Large fragment partly embedded in matrix, recorded by Lang (1922 : 197) and figured by Larwood (1962, pl. 17, fig. 3), labelled " Maastricht, Old collection ", but certainly from a locality of the Cotentin–Maastrichtian, Manche, France.

D.49724. Small bilaminar fragment with three ovicelled zooecia. Upper Maastrichtian, Chef du Pont, Cotentin, Manche, France. Collection E. Voigt.

D.49725. Young unilaminar zoarium with some damaged zooecia. Horizon and locality as above. Collection E. Voigt.

Some fragments. Horizon and locality as above. In Collection E. Voigt, Hamburg, Nr. 3585 and 3924.

III. POLYZOA FROM JURASSIC BEDS WHICH HAVE BEEN REFERRED TO THE CHEILOSTOMATA

It is now evident that the above mentioned Cheilostomata are not Jurassic. There are scattered records in the literature of Cheilostomatous Polyzoa whose Jurassic age is undoubted. In all such cases suspicion rises that they are not Cheilostomata. The fallibility of many of these records depends on the progress of science and today nobody can take seriously mention of Cheilostomatous genera like *Hippothoa, Eschara, Cellaria* or *Cellepora* etc. from the Jurassic by early authors. However, Gregory (1894 : 61) in his note on the Jurassic Cheilostomata considered *Eschara ranvilliana* Michelin from the Bathonian of Ranville, and *Cellaria smithi* Phillips from the Cornbrash of Scarborough, as true Cheilostomata and cited them in support of his theory of the existence of Jurassic Cheilostomata. In his Catalogue of the Jurassic Bryozoa (1896 : 56 and 127) *Cellaria smithi* Phillips is assigned to *Stomatopora* and *Eschara ranvilliana* Michelin to *Diastopora* with no mention that they were regarded as Cheilostomes by himself two years earlier.

F. D. Longe (1881) was still convinced that *Eschara ranvilliana* Michelin from the Bathonian of Ranville belonged to the Cheilostomata when he wrote: " It is perfectly clear, however, that some of the Oolitic *Escharoids* themselves possess the characteristic cell features of the Cheilostomata in a marked degree; and their affinity to the Cheilostomatous *Escharidae* has been recognized by no less authorities than d'Orbigny and Michelin ".

He gave a detailed analysis of the supposed cheilostomatous features of this species and related forms, and tried to derive the Cheilostomata from certain Oolitic Diastoporids whose zooecia remind one, by their oval or polygonal shape, of the Cheilostomata. (" The decumbent cells in *Diastopora* may be regarded as ancestral Cheilostomatous cells, and *Diastopora* itself as the parent stock from which many, if not all, of the families of the Chalk and subsequent periods, grouped as *Cheilostomata*, have been derived ".).

Walford (1894) published a note " On Cheilostomatous Bryozoa from the Middle Lias ". Under the new generic name *Cisternifera* he described some species of cyclostomatous Bryozoa with large heterozooecia—so-called " cistern-cells "—whose relationship with the ovicells of the Cyclostomata was already assumed by Walford. They were thought to bear, occasionally, minute avicularia on the upper lip of the zooecia. Apart from the question of whether these structures are avicularia or not, the different forms attributed to *Cisternifera* are true Cyclostomata, and Gregory (1896) himself has distributed them amongst the genera *Diastopora* and *Entalophora*.

Cellepora davaiacensis Lissajous 1923 from the Bathonian of the Macon district (France), from whose generic name one would expect it to be a Cheilostomatous Polyzoan, and which Lissajous has compared with the Cheilostome *Cellepora polythele* Quenstedt, has been recognized by David (1952) as belonging to the Calcispongia, probably of the genus *Synopelta* Zittel. The list of literature on Jurassic Polyzoa published by David (1960) contains many references to records of Cheilostomata in other works.

From these investigations it is now certain that all supposed species of Jurassic Cheilostomata prove to be mistaken identifications or erroneous stratigraphic records.

IV. ON THE ORIGIN OF GREGORY'S " JURASSIC CHEILOSTOMATA "

In the Cotentin (Manche) Upper Maastrichtian a lithology similar to the " Tuffkreide " from Maastricht itself has long been known. The facies in the Cotentin is a " tuffaceous " detrital limestone with remains of many Foraminifera, Polyzoa, Echinoderms, Brachiopods (Craie à Thécidées ") or hard limestones (Craie à Baculites). It is true that certain blocks of these rocks can be easily mistaken for genuine " Maastrichter Tuffkreide ", because many of the small fossils which make up the rock are common to both strata.

An important difference is the absence of any larger foraminifera like *Orbitoides*, *Lepidorbitoides*, *Siderolites* or *Omphalocyclus* etc. which are distinctive of the Upper Maastrichtian in Holland and Belgium. Hofker (1959) in his monograph on the Foraminifera of the Cotentin Maastrichtian has shown that these beds must be intermediate in age between horizons Cr 4 and Mb in the terminology of Uhlenbroeck for the Upper Cretaceous in South Limburg. This would indicate a stratigraphic position between the phosphatic chalk of Ciply and the base of the Tuffaceous chalk of St. Symphorien in the Mons basin, or an equivalent of the higher beds of Folx-les-Caves and Orp-le-Petit in northern Belgium. This could explain the lack of larger Foraminifera in this region which did not invade the northern regions before the higher horizons of the Maastrichtian. The Maastrichtian age is based upon the occurrence of *Scaphites constrictus* J. Sowerby in the area of Valogne. For the other fauna see Vieillard & Dollfus 1875.

In 1957 I visited the Cotentin region in order to study the classic Senonian localities of d'Orbigny (1850–54) who had described from here, chiefly from Néhou and from Sainte Colombe, some hundred species of Polyzoa. Although there were no extant exposures in the immediate neighbourhood of these villages, some larger quarries near Fresville and Port Filiolet and an excavation for the dairy of Chef du Pont supplied material which furnished examples of a considerable part of the Maastrichtian Polyzoa which were described and figured by d'Orbigny. (For the site

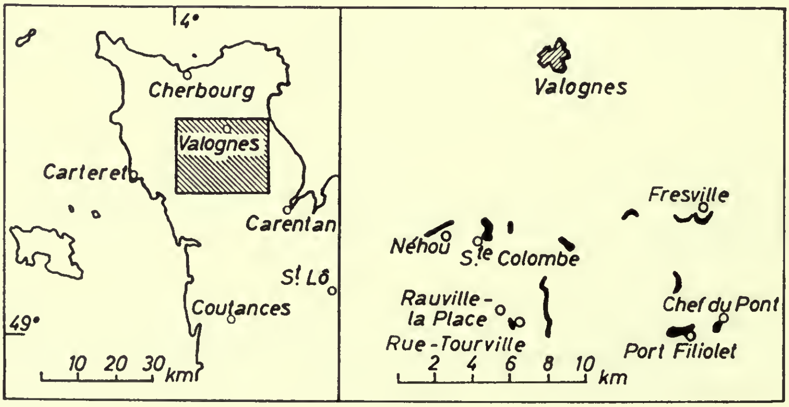

Fig. 1. Map of the outcrops (black) and the localities of the Maastrichtian in the Cotentin area (Normandy). (After Carte géologique detaillée de la France (1 : 80000) Feuille 28, St. Lô (2 éme Ed.) 1926.

of these localities see Text-fig. 1.) This material was augmented by some samples given by Dr. F. Schmid (Hannover) and Polyzoa from Fresville presented by Dr. P. Marie (Paris). It is interesting that many different and new forms not mentioned by d'Orbigny were found at these localities, and by contrast, a large number of d'Orbigny's species could not be found again. Perhaps there are some horizons with a different fauna, and the beds of Sainte Colombe and Néhou may belong to such levels, whose exposures are abandoned today, or the different localities represent heterogeneous ecologic biotopes.

The Polyzoan fauna of this region is the most important one in the northern area and its knowledge is fundamental to our knowledge of the Maastrichtian Polyzoa. With the exception of the inadequate revision of the Cretaceous Polyzoa of d'Orbigny as a whole, which was undertaken by Pergens (1889) and by Canu (1900), nobody has concerned himself with the Polyzoan fauna of the Cotentin for 110 years. An up-to-date revision of this fauna is therefore an urgent task, but it cannot be undertaken without a re-study of d'Orbigny's types which are preserved in the Musée d'Histoire naturelle in Paris.

The most obvious obstacle for a successful revision is the fact that many of d'Orbigny's type specimens are missing, or, if specimens are present, it is often impossible to say with certainty whether they are true " types " or not. On the other hand many of the drawings do not agree well with the originals; they may be stylized, restored or improved and consequently it is often rather difficult to give a satisfactory identification of d'Orbigny's species (see Canu 1900 : 335). His omission to specify the exact locality of the figured specimen in cases when there is more than one such locality, increases the difficulty of identifying the types. There are about 300 photographs of d'Orbigny's polyzoan types of the Paléontologie Française in the author's collection, and this stock, together with a rich collection of French Cretaceous Polyzoa, are the basis for the following discussion.

The proofs for a Cotentin origin for Gregory's " Jurassic Cheilostomata " are:

1. The matrix of sediment adhering to Gregory's originals is identical to that of the above-listed Maastrichtian localities of Cotentin. The matrix detached from block D.181 with *Onychocella piriformis* Goldfuss has yielded two specimens (BB.42981–82) of the characteristic fossil *Thecidea papillata* V. Schlottheim (pl. 1, figs. 9–10) and it is evident that it has been collected from the so-called " Craie à Thécidées " of the Cotentin.

2. The objection that this brachiopod is also common at Maastricht and in Belgium in a similar facies is weakened by the fact that the accompanying fauna in this block, consisting of thirty-one species of Polyzoa, contains some species which are confined to the Cotentin fauna and have never been found in Holland and Belgium, although indeed both strata have many species in common. Examples of species not known from these countries are: *Multicrescis laxata* d'Orbigny, *Membranipora unipora* Marsson, *Stamenocella* cf. *marginata* (d'Orbigny), *Castanopora jurassica* (Gregory), *Onychocella bellona* (d'Orbigny), *Onychocella* cf. *cepha* d'Orbigny, *Onychocellaria caecilia* sp., *Semiescharinella complanata* d'Orbigny, *Lunulites* sp., *Rosseliana thomasi* n. sp., *Frurionella fertilis* n. sp. and others.

3. A Cotentin origin is further suggested by another Cretaceous Polyzoan in the museum collection which is embedded in a typical sample of " Craie à Thécidées ". It is a large specimen of a *Reticrisina*, determined as the Jurassic " *Reticulipora dianthus* (Blainville) " (B.4569 Old collection) and labelled " Bathonian Fresville ". This example gives a good idea of how the error could have arisen: Bathonian rocks being absent near Fresville, Cretaceous Polyzoa were mistaken for Bathonian fossils. Gregory's " Jurassic Cheilostomata " both belong to the Tesson-Collection, which according to Gregory's Catalogue contains many Bathonian Polyzoa from the famous locality of Ranville (Calvados).

The two localities are about 100 km. apart, and it is probable that the labels were confused or that the Cretaceous Polyzoan limestone was mistaken for the not dissimilar Coral and Polyzoan-limestone (" Calcaire à polypiers ") of the Bathonian.

The Tesson-Collection to which Gregory's types belong was acquired in 1857 (Gregory 1896 : 35) and the fossils were probably collected many years ago at a time when geological mapping of this region was still in its infancy.

It is not impossible that Gregory's types both came from Fresville like the *Reticrisina* mentioned above. The rock matrix of D.181 is very like that of the " Craie à Thécidées " of Fresville, but as Dr. Dighton Thomas informed me, that from Chef du Pont is even closer in appearance. But such lithological differences may occur in the same sequence, and are of no great importance.

At least one other possible explanation of this error should be mentioned. Between the Maastrichtian outcrops of Sainte Colombe and Rue Tourville is the village Rauville-la-Place (see Text-fig. 1). Possibly a label " Rauville " was misunderstood for " Ranville ", Calvados.

It must be reckoned that errors like these are more common in old collections, and it may be recalled that a considerable number of Reuss' " Cenomanian Polyzoa of Saxony " came from the Vincentown Limesand in New Jersey (U.S.A.), of Dano-Paleocene age (Voigt 1942). Another mistake is the supposedly new " *Polyphyma bulbosa* " Hamm (1881) from Maastricht which is a Hauterivian form from northern Germany, and which was described in 1839 by Roemer as *Alveolites heteropora* (Voigt 1953 : 57). Certain suspicious anachronisms of phylogenetic level may be explained in this manner as has been shown by the present author with some of Reuss' types.

4. I have collected much material of Bathonian Polyzoa at the classic locality of Ranville (Calvados), but I have never found any trace of Cheilostomata. The objection, that the Cheilostomata may originate in Jurassic times cannot be contested; but we have no remains of them earlier than the Lower Cretaceous. It is true that in the last decade several important groups of fossils have been proved to be older than was formerly assumed. Today we know of Cambrian bivalves, Carboniferous belemnites, Triassic frogs, and these examples could be augmented. It is possible that Jurassic Cheilostomata may be found one day. But in such a case we should expect primitive forms like Membranimorphs as are found in the lower Cretaceous and not highly developed forms like *Onychocella*, or highly specialized forms like the Cribrimorph *Castanopora*.

Lower Cretaceous Cheilostomata are of the greatest phylogenetic interest, and all forms described to date are rare. Most of them are Albian and the oldest is recorded from the Neocomian. Their number is so small that they can be listed in a few lines:

1. *Membranipora neocomiensis* d'Orbigny 1853,
   Neocomian, Saint-Sauveur, Yonne, France. The only specimen was too bad to be figured by d'Orbigny. It must be regarded as a nomen nudum.
2. "*Membranipora*" *constricta* d'Orbigny 1853,
   Aptian, Les Croutes (Yonne).
   Remarks: I have photographed the supposed " type " of this species (pl. 7, fig. 8). It is without doubt a " *Membranipora* " s.l., but it does not correspond with the original figure.
3. *Rhammatopora* (?) *johnstoniana* Mantell 1844,
   Aptian, Lower Greensand, Shanklin-Sand, Kent.
4. *Rhammatopora gaultina* Vine 1890, with his synonyms *Rhammatopora vineï* Lang and *Rhammatopora pembrokiae* Lang (c.f. Thomas & Larwood 1960) Albian-Cenomanian, England.
5. *Charixa vennensis* Lang 1915, Albian, Dorset.
6. *Pyripora texana* Thomas & Larwood 1956, Albian, Texas (U.S.A.).
7. *Wilbertopora mutabilis* Cheetham 1954, Albian, Texas (U.S.A.).

Vine (1890) mentioned *Membranipora fragilis* d'Orbigny, *Membranipora ? obliqua* d'Orbigny, *Membranipora elliptica* v. Hagenow and *Hippothoa simplex* d'Orbigny from the Red Chalk of Hunstanton. The identification of these forms must be revised, but nevertheless all the named species are primitive encrusting membranimorphs of the Division Malacostega, suborder Anasca, and half of them are mono- or oligoserial, and lack either ovicells or avicularia as we must theoretically presume if our ideas about the evolution of the early Cheilostomata are correct. They are followed in the Cenomanian by the first primitive Cribrimorphs and Coilostega with the families of Onychocellidae and Microporidae. Therefore it is hard to understand why Canu & Bassler (1920 : 318) stated that following the Membraniporae, the Acroporidae Canu 1913 (= Porinidae d'Orbigny 1852) of the suborder Ascophora are the most ancient Cheilostome fossils. The main evolution of this family is in the later Upper Cretaceous, and the only described species of *Porina* from the Cenomanian is *P. cenomana* Lecointre (1912) whose origin and inner structure needs revising.

V. PALAEOZOIC CHEILOSTOMATA?

In this connection the question of the systematic position of the north American families Worthenoporidae Ulrich 1893 (Carboniferous) and Palescharidae Miller 1889 (Ordovician-Devonian) cannot be neglected. These were established for the single genera *Worthenopora* Ulrich 1889 and *Paleschara* Hall 1874 which resemble Cheilostome Polyzoa in some features. Ulrich (1890) stated that the affinities of that genus are nearer to the Membraniporidae than any other and that his present views would admit it being placed in the Cheilostomata. Nickles & Bassler (1900) regarded both families without any restriction as Cheilostomata. This classification was followed by many authors, but in recent times this opinion seems to have been abandoned. Bassler (1953) has placed them among the Cryptostomata, but considers *Worthenopora* " may belong among cheilostomes ".

Worthenopora, indeed, has the outward aspect of a Cheilostome with its triangular or semielliptical apertures, with posterior raised margin and spine bases. *Paleschara* with its simple short polygonal zooecia is like a *Membranipora* which possesses completely opened opesiae without any trace of a gymnocyst.

Dr. Dighton Thomas has kindly lent me some specimens of both genera from the museum collection. Although there is no space here to go into details, further studies of this problem are intended. I have got the impression that they cannot be attributed to the Cheilostomata. *Paleschara* must be regarded as a very primitive Cryptostome, and *Worthenopora*, in contrast, as a specialized one. The latter has reached a level of evolution which reminds one of certain Cheilostomata. It has not been found in beds younger than Mississippian, and there are no intermediate forms between it and the Cretaceous Cheilostomata. Consequently it seems to be impossible to regard it as an ancestor of the true earliest membranimorph Cheilostomata of the Lower Cretaceous.

Paleschara, with its network of rather simple polygonal zooecia, may perhaps be primitive enough to give rise to Cheilostomata-like forms. But it could be better regarded as a cryptostomatous form corresponding to a membranimorph level of primitive Cheilostomata.

We have no palaeontological evidence for a descent of the Cheilostomata from the Cryptostomata or from the Ctenostomata. As Borg (1930 : 54) and Cori (1941) regard the Ctenostomata as emanating from primitive Cheilostomata, it must be emphasized that the Ctenostomata are the older group, represented by fossils from the Ordovician onwards and that there is no possibility of deriving the Ctenostomata from the Cheilostomata. Silén (1942) regards the Cheilostomata and the Ctenostomata as closely allied (" Cheilo-Ctenostomata ") and believes that both have common ancestors.

Silén has established an interesting theory about the origin of the Cheilostomata from hypothetical primitive forms like the recent *Labiostomella* which he calls Protocheilostomata. These have erect zoaria with frontal budding and other primitive features, and it would mean that the encrusting growth of many Cheilostomata and the lateral budding as existing in all other Cheilostomata, are secondary. It should be emphasized that the oldest known Cheilostomata from the Lower Cretaceous do not show this primitive character. All are encrusting, and they must already have passed the evolutionary level of the " Protocheilostomata ", which according to Silén were feebly or not at all calcified. If this is admitted, there remains no possibility of regarding *Worthenopora* or *Paleschara* as early Cheilostomata of the Palaeozoic.

VI. THE ACCOMPANYING FAUNA OF THE MATRIX OF GREGORY'S " JURASSIC CHEILOSTOMATA "

It is satisfactory that in the matrix of Gregory's " Jurassic Cheilostomata " are enclosed other Bryozoa which were overlooked by Gregory. In block D.180, containing *Castanopora jurassica*, *Multicrescis laxata* d'Orbigny, *Rosseliana thomasi* n. sp. and *Pliophoea* sp. could also be observed.

I am much indebted to Dr. Dighton Thomas for his permission to remove about 2 cm.^{3} of the matrix of block D.181 with *Onychocella bathonica*. This piece was cracked under a press and the washing of the residue has yielded a fauna of thirty-three species of Polyzoa and one Brachiopod. This fauna is described in detail in the following part of this paper. Most of the treated specimens are figured although the state of preservation is rather poor because the hard rock is unfavourable for clean preparation. All specimens are somewhat damaged, or rolled and, unfortunately, recrystallized or covered with minute calcite crystals as is often observed in the Cotentin material, and it is nearly impossible to stain them with colour. This explains any mediocre photos. In many cases figures of comparable specimens of the same species from the Cotentin are given for comparison. If they do not always present exactly the same picture as the specimens from the original French localities, this is because there often exists a great variability in size or growth-stage, and in preservation, and that the identification is based upon a vast quantity of material. It is surprising that in only 2 cm.^{3} of rock from D.181 some small fragments of new species were found, although these have long been known to the author from the Maastrichtian of the Cotentin. The opportunity is taken here to describe them. But it should not be forgotten that this small fauna from only a few cm.^{3} matrix must represent a very small part of the rich Polyzoan fauna of the Cotentin Maastrichtian, and that its composition is purely accidental.

The list given in table 1, p. 41, contains thirty-three Polyzoan species of which twenty-four are Cheilostomata. It is not complete because in some cases a complete identification could not be made, and for a few forms no identification was possible. Excepting *Pliophloea* sp. all forms have been found by the author in the Maastrichtian of the Cotentin. Twenty-six species were found at Chef du Pont, eighteen at Port Filiolet and nine at Fresville. But it should be taken into account that the investigated material is too poor for important deductions. Many species very common at all Cotentin localities are not represented, and others are new for the Cotentin. The affinities with the classic locality of Maastricht are proved by fourteen species but this figure may be too large because several forms of both regions may be identical. Von Hagenow's types from Maastricht having been lost during the second world war, it is not yet possible to decide this question with certainty.

I. Polyzoa

A. *CYCLOSTOMATA*

Genus ***BERENICEA*** Lamouroux 1821

1. ***Berenicea*** sp.

One small incomplete zoarium which is indeterminable, encrusts *Reteporidea lichenoides* Goldfuss.

Specimens. A minute incomplete zoarium encrusting *Reteporidea lichenoides* Goldfuss (= D.49569).

Genus ***ENTALOPHORA*** Lamouroux 1821

2. ***Entalophora benedeniana*** (von Hagenow)

1851 *Pustulopora benedeniana* von Hagenow: 17, pl. 1, fig. 6.
1899 *Entalophora madreporacea* Goldfuss var. *benedeni* von Hagenow; Gregory: 239.
1964 *Entalophora benedeniana* (von Hagenow) Voigt: 422, pl. 1, figs. 1–7.

One small fragment embedded in matrix has been referred to this well-known species from Maastricht which is represented in the author's collection from the Maastrichtian of Chef du Pont (Manche). For morphological details and ovicells see Voigt (1964).

Specimens. D.49560. One poorly preserved fragment in matrix from D.181. Upper Maastrichtian, Cotentin, Manche, France.

Genus ***IDMIDRONEA*** Canu & Bassler 1920

3. ***Idmidronea macilenta*** (von Hagenow)

1851 *Idmonea macilenta* von Hagenow: 29, pl. 2, fig. 4.
?1851 *Idmonea ramosa* d'Orbigny: 736, pl. 611, figs. 11–15.
1899 *Retecava ramosa* (d'Orbigny) Gregory: 192, pro parte.
1951 *Idmidronea macilenta* Voigt: 38, pl. 4, figs. 14–17.

One small distal fragment of this abundant species of the Upper Maastrichtian belongs to *I. macilenta*. These thin distal branches do not have the numerous firmatopores which are well developed on the reverse side of the broader and older stems. Therefore they are very similar to *Idmonea* (*Tubigera*) *antiqua* Defrance (d'Orbigny 1853 : 722, pl. 613, figs. 11–15, figured under the name of *Stichopora regularis* d'Orbigny). *Idmonea disticha* Goldfuss (sensu von Hagenow 1851 : 30, pl. 2, fig. 8) may be mistaken for this form also, but always it is not so flat as the distal ends of *Idmidronea macilenta*. The species cited by d'Orbigny from Sainte-Colombe under the latter name may be *Idmonea macilenta*.

If this species is con-specific with *Idmonea ramosa* d'Orbigny, the latter name has priority and must be preferred. It is represented at Fresville (Cotentin, Manche).

Stratigraphical range. Upper Maastrichtian.

Specimens. D.49561. A worn fragment from matrix of D.181. Upper Maastrichtian, Cotentin, Manche, France.

D.49843. A fragment, upper Maastrichtian, Chef du Pont, Cotentin, Manche, France. E. Voigt Collection.

Genus ***HETEROCRISINA*** Gabb & Horn 1860, em. Voigt 1964

4. ***Heterocrisina communis*** (d'Orbigny)

1853 *Idmonea communis* d'Orbigny: 745, pl. 750, figs. 6–10.
1887 *Idmonea pseudodisticha* (non von Hagenow) Marsson: 28, pl. 2, fig. 8.
1860 *Heterocrisina* abbottii Gabb & Horn: 404, pl. 69, figs. 45–47.
1899 *Retecava abbottii* (Gabb & Horn) Gregory: 205.
non 1907 *Idmonea abbottii* (Gabb & Horn) Ulrich & Bassler: 321, pl. 22, figs. 3–4.
1964 *Heterocrisina communis* (d'Orbigny) Voigt: 432 pl. 3, figs. 1–10.

Two small worn fragments belong to this species, which is very distinctive because of its large frontal ovicell, although it has often been mistaken for other species. For further information about its generic position and morphological details see Voigt (1964).

This form is common at all Maastrichtian localities in the Cotentin (Fresville, Port Filiolet and Chef du Pont).

Stratigraphical range. Campanian-Maastrichtian.

Specimens. D.49562-63. From matrix of D.181. Upper Maastrichtian, Cotentin, Manche, France.

Genus *CRISISINA* d'Orbigny 1847

5. *Crisisina carinata* (Roemer)

(Pl. 1, figs. 4–5)

1840 *Idmonea carinata* Roemer: 21, pl. 5, fig. 20.
1964 *Crisisina carinata* (Roemer) Voigt: 429, pl. 4, figs. 1–7. (See full references.)

Three worn fragments belong to this very common and widespread species of the Upper Cretaceous. The synonymy is very confused—see Voigt (1964)—where all known synonymies are given and the generic classification is discussed.

Very abundant at all Maastrichtian Cotentin localities.

Stratigraphical range. Cenomanian-Paleocene.

Specimens. D.49564-66. From matrix of D.181. Upper Maastrichtian, Cotentin, France.

D.49567. A fragment for comparison with D.49566. Upper Maastrichtian, Port Filiolet, Cotentin, Manche, France, Voigt Collection.

Genus *OSCULIPORA* d'Orbigny 1847

6. *Osculipora truncata* (Goldfuss)

1826 *Retepora truncata* Goldfuss: 28, pl. 9, fig. 14.
1851 *Truncatula truncata* (Goldfuss) v. Hagenow : 35, pl. 3, fig. 2.
1851 *Truncatula tetrasticha* von Hagenow: 34, pl. 3, fig. 3.
1909 *Osculipora truncata* (Goldfuss) Gregory: 58.
1922 *Osculipora truncata* (Goldfuss) Canu & Bassler: 57, pl. 23, figs. 1–6.

One small worn fragment may be referred to *O. truncata*; it is in the condition of *Truncatula tetrasticha* von Hagenow, which represents highly worn branches of *O. truncata* (Goldfuss.)

Further investigations are necessary to check whether the older citations of this form from the Cenomanian by Reuss (1872) are correct. In the author's collection from Chef du Pont, Port Filiolet and Fresville are numerous fragments of this species, which was not recorded by d'Orbigny from any of his Cotentin localities.

Stratigraphical range. Cenomanian (?) to Maastrichtian.

Specimens. D.49568. A very poorly preserved worn fragment from the matrix of D.181. Upper Maastrichtian, Cotentin, Manche, France.

Genus *RETEPORIDEA* d'Orbigny 1849

7. *Reteporidea lichenoides* (Goldfuss)

1826 *Retepora lichenoides* Goldfuss: 29, pl. 9, figs. 13a–b.
1851 *Idmonea lichenoides* (Goldfuss) von Hagenow: 28, pl. 2, fig. 6.
1899 *Retecava lichenoides* (Goldfuss) Gregory: 194, fig. 16, p. 195.

One very poor fragment which is encrusted by a small young *Berenicea*, has been recognized as this species which is very abundant in the Upper Maastrichtian. It is represented in the author's collection from Port Filiolet by some specimens. It has not previously been recorded from the Cotentin Maastrichtian.

STRATIGRAPHICAL RANGE. Maastrichtian.

SPECIMENS. D.49569. A small worn fragment with an encrusting *Berenicea* from the matrix of D.181. Upper Maastrichtian, Cotentin, Manche, France.

Genus *PETALOPORA* Lonsdale 1850

8. *Petalopora* sp.

(Pl. 1, figs. 1–3)

There are a few fragments of a badly preserved *Petalopora* which are conspecific with similar specimens from Chef du Pont (pl. 1, fig. 2). Their identification involves some difficulties because it is impossible to identify them from published figures. They are allied to *Heteropora reticulata* Marsson (1887 : 26, pl. 2, fig. 4) in the size of the branches and diameter of the apertures (about 0·14–0·15 mm.), but the mesopores are much less conspicuous, and on the figured fragment (pl. 1, fig. 1) they look a little like longitudinally-oriented lines which are straight or sinuously bent and interspersed between fine ribs. On the specimen from Chef du Pont the mesopores are larger and they show a more longitudinally-oriented inconspicuous network (pl. 1, fig. 3). I have no doubt that these three specimens are conspecific in spite of this difference but I dare not identify them with any known species.

SPECIMENS. D.49570–72. Three small worn fragments from the matrix of D.181. Upper Maastrichtian, Cotentin, Manche, France.

D.49573. A larger fragment from the matrix of D.181. Upper Maastrichtian, Cotentin, Manche, France.

D.49574. A larger fragment. Upper Maastrichtian, Port Filiolet, Cotentin, Manche, France. Voigt Collection. One branched fragment. Upper Maastrichtian, Chef du Pont, Cotentin, Manche, France. Voigt Collection, Hamburg, Nr. 3969.

Genus *MULTICRESCIS* d'Orbigny 1854

9. *Multicrescis laxata* d'Orbigny

(Pl. 1, figs. 6–8)

1854 *Multicrescis laxata* d'Orbigny: 1077, pl. 800, figs. 10–11.

HOLOTYPE. Upper Maastrichtian, Sainte Colombe, Cotentin, Manche, France. d'Orbigny Collection, Paris, Musée d'Histoire Naturelle Nr. 8416.

There is a fragment of a "heteroporid" Polyzoan with an encrusting colony of *Rosseliana thomasi* n. sp. embedded in the matrix of *Castanopora jurassica* Gregory (D.181). It cannot be distinguished from d'Orbigny's type specimen of *Multicrescis laxata,* whose apertures and the mesopores are exactly the same. Unfortunately there are no other specimens of this species in d'Orbigny's collection which would allow confirmation of the inner structures by sections. Specimens from Chef du Pont (Manche), which seem to be conspecific with d'Orbigny's species have a median lamella like *Grammascosoecia* Canu & Bassler 1922. Pergens (1889 : 373) and Canu & Bassler (1922 : 119) have included this species in the synonymy of *Grammascosoecia dichotoma* (Goldfuss) from Maastricht (see von Hagenow 1851 : 47, pl. 5, fig. 15). This might be correct; some specimens from Fresville can hardly be distinguished from the Maastricht species. On the other hand there are some fifty fragments from Fresville, and none show the characteristic pattern of small regular smooth quadrangles which grow from the calcified mesopores (cf. von Hagenow's fig. 15i and Voigt 1951 pl. 4, fig. 1) and which can be observed in the majority of the Maastricht specimens. Therefore I still hesitate to unite it with *Grammascosoecia dichotoma* (Goldfuss).

D'Orbigny attributed his species to his genus *Multicrescis* which is multilamellar. But this is not the case in *M. laxata,* although d'Orbigny noted two layers in his type-specimen from Sainte-Colombe, which is a basal fragment (pl. 1, figs. 7–8). It is well known that the basal stems often develop more than one layer of zooecia, and therefore there is no reason to place this form in the genus *Multicrescis.* Many specimens from Fresville have radiating rows of peristomes as in *Multicavea,* which can also be observed in *Grammascosoecia dichotoma* (Goldfuss). But the ovicell of the Cotentin form has not yet been discovered. Therefore I prefer to leave this form provisionally under the name given by d'Orbigny.

It should be noted that the median lamella in *Grammascosoecia dichotoma* (Goldfuss) is not constant. It is lacking in many specimens from Maastricht, and there is no reason to assume a different species.

STRATIGRAPHICAL RANGE. Upper Maastrichtian.

SPECIMENS. D.49575. A worn fragment with encrusting *Rosseliana thomasi* n. sp. embedded in matrix of *Castanopora jurassica* (Gregory) (D.180). Upper Maastrichtian, Cotentin, Manche, France. Labelled erroneously by Gregory as "Bathonian, Ranville, Calvados".

B. *CHEILOSTOMATA*

MEMBRANIPORA Blainville 1830 (sensu lato)

10. "***Membranipora***" ***unipora*** (Marsson)

(Pl. 2, figs. 7–8)

1852 *Flustrella simplex* d'Orbigny: 293, pl. 699, figs. 14–16.
1887 *Biflustra unipora* Marsson: 52.
1929 *Membranipora genucia* Brydone: 37, pl. 13, figs. 10–11.

1930 *Membranipora unipora* (Marsson): Voigt 420, pl. 4, fig. 5.
1925 *Membranipora unipora* (Marsson): Levinsen 329, pl. 2, fig. 22.

HOLOTYPE. Upper Maastrichtian, Néhou, Cotentin, Manche, France. d'Orbigny Collection, Paris. Musée d'Histoire Naturelle Nr. 8130.

One unilaminar specimen embedded in matrix, showing some zooecia with the characteristic avicularium on the gymnocyst below the opesia and the narrow helmet-shaped hyperstomial ovicell, agrees very well with d'Orbigny's type from Néhou (pl. 2, fig. 8) and another well preserved specimen from the Maastrichtian of Port Filiolet (Manche). The zoarial length is from 0·80–1·20 mm. The spines of the well raised margin of the opesia, which is 0·45–0·50 mm. long, number about twenty, but they are inconspicuous and often hidden by recrystallization of calcite. The zooecia and the opesiae of my specimen of this species from Port Filiolet are a little larger than those of the Museum-specimen but this lies within the range of variation of this form. *Membranipora genucia*, described by Brydone from the upper Campanian of Meudon near Paris, is a synonym as shown by comparison with Cotentin and Rügen specimens with those from Meudon.

Marsson who translated this species from *Flustrella* to *Biflustra*, has changed the species name *simplex* to *unipora* because there existed already a recent *Biflustra simplex* d'Orbigny 1839. Otherwise another Cretaceous *Membranipora simplex* d'Orbigny exists too. It is clear that the placing of this species in " *Membranipora* " is only provisional; a revision of the Cretaceous Membraniporae might put it in another genus.

STRATIGRAPHICAL RANGE. Upper Campanian-Maastrichtian.

SPECIMENS. D.49576. Fragment with ovicelled zooecia from the matrix of D.181. Upper Maastrichtian, Cotentin, Manche, France.

Genus *AMPHIBLESTRELLA* Prud'homme 1960

11. *Amphiblestrella elegans* (von Hagenow)

(Pl. 4, figs. 1–3)

1851 *Siphonella elegans* von Hagenow: 84, pl. 6, fig. 7.
1851 *Flustrella baculina* d'Orbigny: 291, pl. 699, figs. 4–6.
1930 *Amphiblestrum elegans* (von Hagenow) Voigt: 448, pl. 13, figs. 13–16.
1960 *Amphiblestrella elegans* (von Hagenow): Prud'homme: 949.
1962 *Amphiblestrum elegans* (von Hagenow) Berthelsen: 100, pl. 9, figs. 1–5.

There is only one small fragment which is 1·7 mm. long and shows eight rows of zooecia; normally there are ten to sixteen. The zoarial dimensions are smaller than those of specimens from the type-locality of Maastricht, and from the Cotentin, where this species is very common. The axial canal of the hollow zoaria, clearly visible in the thicker zoaria, is much reduced in the slender branches, and may disappear almost completely as shown in d'Orbigny's type specimen of his *Flustrella baculina* (pl. 4, fig. 2) from Néhou. The zooecia from Danian material are mostly longer than those from the Maastrichtian (about 0·7 mm. instead of 0·6 mm.). The size of the opesiae is very variable in this species. Canu (1900) in his revision of d'Orbigny (1851–54) has incorrectly regarded this species as a synonym of *Flustrella irregularis* d'Orbigny.

In the Cotentin localities this species is represented from Fresville and Chef du Pont and by d'Orbigny's type specimen of *Flustrella baculina* from Néhou.

STRATIGRAPHICAL RANGE. Maastrichtian-Danian.

SPECIMENS. D.49577. A worn fragment from matrix of D.181. Upper Maastrichtian, Cotentin, Manche, France.

D.49578. A well preserved branched fragment. Upper Maastrichtian, Chef du Pont, Cotentin, Manche, France. Voigt Collection.

Type-specimen of *Flustrella baculina* d'Orbigny. Upper Maastrichtian Néhou, Cotentin, Manche, France. In d'Orbigny Collection, Paris, Musée d'Histoire Naturelle Nr. 8127.

Genus ***RADULOPORA*** nov.

DERIVATIO NOMINIS. Derived from the species-name of *Biflustra radula* Marsson 1887.

DIAGNOSIS. Zoarium bilaminar, dichotomously branched and probably radicelled at the base. Zooecia dimorphic, the marginal zooecia of the acute edges of the branches being larger, and having larger opesiae than the normal zooecia. Cryptocyst well developed, finely granulated; opesiae small with straight proximal rim and occasionally developed lip. Distal interzooecial asymmetrical vibracula above the opesiae with long elliptical opening and a small thornlike process going out from the left or right inner margin. Ovicells inconspicuous exteriorly, deeply immersed, endozooecial.

Type species: *Biflustra radula* Marsson 1887, Lower Maastrichtian Rügen (Germany).

REMARKS. This new genus comprises three characteristic species in the Maastrichtian, which cannot be attributed to any other genus hitherto known. *Biflustra radula* Marsson was assigned incorrectly to *Amphiblestrum* by Voigt (1930). It differs from *Amphiblestrum* not only in its bilaminar and apparently radicelled zoarium with dimorphic zooecia and semicircular opesia in which a proximal lip is originally developed, but also by its avicularian-like vibraculum. This has no pivot for the articulation of the mandibula as in true avicularia, but asymmetrical curved thorn-like processes on the inner left or right edge of the vibracula (Text-fig. 2) and an ellipsoidal cavity in the proximal part adapted for the motion of the seta of the vibraculum. These structures are very well shown in the type-species, *R. radula* (Marsson) (pl. 3, figs. 11–12), while they are indicated in *R. minor* only in some better preserved specimens.

Owing to the loss of the Marsson Collection during the last war, a neotype for *R. radula* Marsson should be erected. The specimen of *Biflustra radula* figured here could represent a good neotype, but it was collected from a chalk block in glacial drift and therefore a topotype from the Lower Maastrichtian of Rügen would be preferred.

It is difficult to decide if this genus should be regarded as belonging to the Malacostega or Coilostega. The cryptocyst is strongly calcified and the opesia is so small that the Malacostega level has probably been exceeded. Opesiules are absent as in many Coilostega. Nevertheless Marsson described it as *Biflustra*, and perhaps he was right to assign it to the Membranimorphs, although there are many intermediate forms between these two groups. This genus seems to be rather isolated and it is difficult to attribute it to one particular family of the Malacostega.

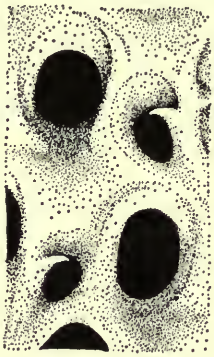

FIG. 2. *Radulopora radula* (Marsson). Some zooecia and vibracularia. ×60.

12. ***Radulopora minor*** sp. n.

(Pl. 3, figs. 6–10)

Holotype Upper Maastrichtian, St. Pietersberg near Maastricht (Netherlands). D.49844. Voigt Collection.

DERIVATIO NOMINIS. The name refers to the smaller zooecial dimensions in contrast to the type-species *R. radula* (Marsson) (pl. 3, figs. 11–12).

DIAGNOSIS. *Radulopora* with slender dichotomous branches 0·7–1·2 mm. wide, consisting of about three to seven alternating transverse rows of zooecia about 0·5–0·6 mm. long. The edges of the zoarium are formed by the larger marginal zooecia: other zooecia not clearly distinct at their margins, elongate and pyriform with distal raised margin and a well developed cryptocyst deeply immersed proximally. Opesiae rounded quadrangular or high-semicircular rounded distally and truncated proximally, showing in some specimens a well developed proximal lip. Distal vibracula small, the peak turned obliquely downwards but symmetrically oriented outwards from the median line toward the edges of the branches. Ovicells form inconspicuous slight swellings above the opesiae (pl. 3, fig. 9).

DESCRIPTION. The bilaminar fronds have narrow cylindrical or prismatic basal rods which are pointed toward their proximal ends and suggest an articulated basal attachment of the zoarium. The zoarial and opesial dimensions are smaller in these proximal parts of the zoarium than in the more distal branches. The shape of the opesia varies from nearly semi-circular to high-oval, trapezoidal or oval: if it is oval it is narrowed proximally but it is never circular. The straight proximal edge of the opesia is deeply immersed in old zooecia and may disappear. The distinct proximal lip observed regularly in some specimens has its origin from this straight proximal edge. The opesia occupies about one quarter to one fifth of the length of the zooecium. The cryptocyst is highly calcified and often appears in the proximal part. The marginal zooecia appears to be larger than they actually are because they are not narrowed in their proximal part, and the opesiae are always distinctly larger than in the other zooecia, although there may be transitions between the size of the opesiae of the normal and those of the marginal zooecia. The ovicelled zooecia never have vibracula. The ovicells are very flat swellings above the opesiae. If their roof is broken away a large deep hollow is revealed showing that the ovicell is deeply immersed although it must be regarded as endozooecial.

A minute fragment of eight zooecia belongs to this species which corresponds very well with the abundant material of the author's collection from the Cotentin localities and from Maastricht.

MEASUREMENTS.

Lz (= Distance between the opesia): 0·50–0·67 mm.

$$\left.\begin{array}{l}\text{ho} = 0{\cdot}10\text{–}0{\cdot}12 \text{ mm.}\\ \text{lo} = 0{\cdot}075\text{–}0{\cdot}12 \text{ mm.}\end{array}\right\}\text{normal zooecia.}$$

$$\left.\begin{array}{l}\text{ho} = 0{\cdot}14\text{–}0{\cdot}17 \text{ mm.}\\ \text{lo} = 0{\cdot}15\text{–}0{\cdot}16 \text{ mm.}\end{array}\right\}\text{marginal zooecia.}$$

STRATIGRAPHICAL RANGE. Upper Maastrichtian.

SPECIMENS. D.49579. A small worn fragment. From matrix of D.181. Upper Maastrichtian, Cotentin, Manche, France.

D.49580–81. Two fragments. Upper Maastrichtian, Chef du Pont, Cotentin, Manche, France. Voigt Collection.

D.49582. Fragment with ovicelled zooecia. Upper Maastrichtian, Cotentin, Manche, France. Voigt Collection.

Genus ***HAGENOWINELLA*** Canu 1900

13. ***Hagenowinella*** cf. ***incrassata*** (d'Orbigny)

(Pl. 2, figs. 1–3)

1853 *Flustrellaria incrassata* d'Orbigny: 527, pl. 726, figs. 5–8.

A large unilaminar fragment consisting of more than twenty zooecia may belong to this species, although the opesiae are oval and not so broad and truncated as in d'Orbigny's type-specimen from Sainte-Colombe (Manche). A fragment of this form collected by the author near Chef du Pont (Manche), shows, however, that the shape of the opesiae can vary considerably and that in certain parts of the zoarium the opesiae are fairly oval as in D.49583, in which two zooecia have the cryptocyst broken giving the false appearance of avicularia. The hyperstomial ovicells shown on the specimen from Chef du Pont are broad and low. The horse shoe-like lamella in the interior of the zooecia seems to be hidden by a fine calcitic crust, but it is indicated in pl. 2, figs. 2–3, by two small knob-like processes at the inner margin of the opesia.

Specimens. D.49583. A small fragment of zoarium, embedded in matrix of D.181. Upper Maastrichtian, Cotentin, Manche, France.

D.49845. Fragment of zoarium. Upper Maastrichtian, Fresville, Cotentin, Manche, France. Voigt Collection. Fragment with ovicelled zooecia. Upper Maastrichtian, Chef du Pont, Cotentin, Manche, France. Voigt Collection, Hamburg, Nr. 3909.

Stratigraphical range. Upper Maastrichtian.

Genus *BACTRELLARIA* Marsson 1887

14. *Bactrellaria rugica* Marsson

(Pl. 2, figs. 9–14)

1887 *Bactrellaria rugica* Marsson 59, pl. 5, fig. 18.
1930 *Bactrellaria rugica* Marsson; Voigt: 444, pl. 12, figs. 25–26.

The species is represented by one very poor fragment showing four zooecia of the frontal face with worn avicularia forming cavities between the opesiae. Although the specimen is very small and worn, the species is so characteristic that there is no doubt about the identification. It has been found by the author at Maastricht and Port Filiolet (Manche) where it is rare. The frontal avicularium below the opesia is, if well preserved, rather prominent, elongate beak-like and is proximally oriented with a raised spatulate peak. Marsson's figure showing only a round pore is inadequate, but he makes mention of the tube-like avicularia which occasionally occur on the lateral edges of the zoaria. The frontal avicularium below the opesia, is, if present and well preserved, rather prominent, tube-like, elongate and proximally oriented. Its beak is dilated and spatulate but is mostly broken away or damaged. It is rather well preserved on a specimen from an Upper Maastrichtian chalk-bearing erratic flint-boulder found in the gravel-pit of Wulmstorf near Harburg (pl. 2, fig. 13). If the dilated spatulate avicularian beak is destroyed there remains an oval ring or a scar like the ones in many specimens of the Cotentin (pl. 2, figs. 9 and 12). The small pit on Marsson's figure, however, is not the cicatrix of a destroyed avicularium, but corresponds to the spot where the avicularium is usually developed. Three pairs of oral spines are present in well preserved specimens. The ovicells are hyperstomial. Many fragments of the band-like zoaria from the Cotentin localities have four to six rows of zooecia instead of three; their diameter varies between 0·7–2·0 mm. The length of the zooecia is between 0·6–0·8 mm., that of the opesia *c.* 0·35 mm. In addition to the band-like specimens there occur, at Maastricht, prismatic vincularian rods with five or more rows of zooecia showing absolutely the same features and size of zooecia, avicularia and ovicells. They are very like *Pithodella* and it is possible that they represent another mode of growth of the same species. *Eschara gaimardi* von Hagenow (1851 : 82, pl. 12, fig. 10) is thought to be an *Eschara-like* stem development of this genus.

Stratigraphical range. Maastrichtian.

Specimens. D.49584. A small worn fragment. From matrix of D.181. Upper Maastrichtian, Cotentin, Manche, France.

D.49585. A well preserved fragment. Upper Maastrichtian, Port Filiolet, Cotentin, Manche, France. E. Voigt Collection. A worn fragment. Upper Maastrichtian, Port Filiolet, Cotentin, Manche, France. Voigt Collection, Hamburg Nr. 3914.

A well preserved fragment. Upper Maastrichtian Chalk from Flint-boulder in Pleistocene Drift. Wulmstorf near Harburg-Hamburg, Germany. Voigt Collection Nr. 4146.

Genus *STAMENOCELLA* Canu & Bassler 1917

15. *Stamenocella marginata* (d'Orbigny)

(Pl. 3, figs. 1–5)

1852 *Flustrella marginata* d'Orbigny: 295, pl. 700, figs. 7–9.
1852 *Flustrella convexa* d'Orbigny: 290, pl. 699, figs. 1–3.
1852 *Biflustra tesselata* d'Orbigny: 271, pl. 694, figs. 7–9.

HOLOTYPE. A small fragment of *Flustrella marginata* d'Orbigny. Upper Maastrichtian, Sainte Colombe, Cotentin, Manche, France. In d'Orbigny Collection, Paris, Musée d'Histoire Naturelle, Nr. 8134.

A worn fragment of this species embedded in the matrix of *Onychocella bathonica* Gregory (D.181) agrees in all essential characteristics with the two specimens which were described by d'Orbigny as *Flustrella marginata* from Sainte-Colombe and *Biflustra tesselata* from Néhou, and which are figured here for comparison. The latter is a worn specimen of *Stamenocella marginata* showing traces of ovicells and represents the same stage of preservation as figs. 3 and 8 of pl. 31 of Canu & Bassler (1920) where the ovicells and the avicularia of *Stamenocella mediaviculifera* and *Stamenocella inferaviculifera* cause two shallow cavities between the opesiae.

Pl. 3, fig. 5, shows a rather well preserved specimen which seems to be intermediate between *Flustrella marginata* d'Orbigny and *Flustrella convexa* d'Orbigny. The basal region, which tapers proximally and shows a radicelled base, has zooecia corresponding to those of *Flustrella convexa*. They are closed by a calcareous lamella and pierced by elliptical or round openings as can also be observed in other species of *Stamenocella*.

The variation in the size of the opesiae is enormous in this species as shown in pl. 3, fig. 5, and the following measurements:

$L_z = 0{\cdot}50\text{–}0{\cdot}63$ mm.
$l_z = 0{\cdot}17\text{–}0{\cdot}25$ mm.
$L_o = 0{\cdot}17\text{–}0{\cdot}33$ mm.
$l_o = 0{\cdot}07\text{–}0{\cdot}15$ mm.

STRATIGRAPHICAL RANGE. Maastrichtian.

SPECIMENS. D.47322. A fragment embedded in the matrix of *Onychocella bathonica* Gregory (D.181). Upper Maastrichtian, Cotentin, Manche, France.

D.49586. A fragment from the matrix of D.181. Upper Maastrichtian, Cotentin, Manche, France.

D.49587. A small worn fragment. Locality and horizon as above. A well preserved fragment showing the stage of *Flustrella convexa* d'Orbigny at the base of the zoarium. Upper Maastrichtian, Chef du Pont, Cotentin, Manche, France, Voigt Collection, Hamburg, Nr. 4128.

Type specimen of *Biflustra tesselata* d'Orbigny. Upper Maastrichtian, Néhou, Cotentin, Manche, France. d'Orbigny Collection, Paris, Musée d'Histoire Naturelle. Nr. 8053.

Genus *THYRACELLA* Voigt 1930

16. ***Thyracella*** cf. ***meudonensis*** (d'Orbigny)

(Pl. 2, figs. 4–6)

cf. 1851 *Biflustra meudonensis* d'Orbigny: 263, pl. 692, figs. 4–6.
1951 *Thyracella* cf. *meudonensis* (d'Orbigny) Voigt: 59, pl. 9, figs. 4–5.

Three fragments of this bilaminar species are conspecific with a "*Biflustra*" which is very abundant in the Maastrichtian of Port Filiolet (Manche). It has a very prominent large avicularium as is typical of *Thyracella* (pl. 2, fig. 4). I think it could be identified with *Biflustra meudonensis* d'Orbigny recorded by him from Néhou and Meudon. In the catalogue of the d'Orbigny collection only one fragment from the Chalk of Meudon is registered under Nr. 8090 although I possess more than fifty specimens from this locality which would fit very well into that species. It is worn and does not correspond with the figure; it does not look like a chalk fossil from Meudon, but seems to have come from a more littoral facies resembling the Maastrichtian of the Cotentin. The worn specimens, described and figured by the present author from the Maastrichtian of Kunrade (S-Limburg) and Ilten (northern Germany) give a different impression from that of the well preserved material from the Cotentin localities in the author's collection. But there are all intermediate stages. For comparison a photograph of a characteristic specimen with a large avicularium, from Port Filiolet (Manche), is given (pl. 2, fig. 4). The length of the avicularium is *c.* 0·8 mm., and that of the zooecia *c.* 0·5–0·6 mm. The well preserved zooecia always have a sharp and distinct margin in the distal part as shown in the figure of d'Orbigny.

STRATIGRAPHICAL RANGE. Maastrichtian and (fide d'Orbigny) Upper Campanian.

SPECIMENS. D.49588. A damaged fragment from the matrix of D.181. Upper Maastrichtian, Cotentin, Manche, France.

D.49846. A fragment embedded in matrix of D.181. Upper Maastrichtian, Cotentin, Manche, France.

D.49589–90. Two fragments from the matrix of D.181. Upper Maastrichtian, Cotentin, Manche, France.

A well preserved branched fragment with an avicularium. Upper Maastrichtian, Port Filiolet, Cotentin, Manche, France. Voigt Collection, Hamburg. Nr. 3919.

A worn fragment labelled Meudon but likely. Upper Maastrichtian, locality uncertain (? Néhou, Cotentin, Manche). d'Orbigny Collection, Paris, Musée d'Histoire Naturelle Nr. 8040.

Genus *VINCULARIA* (auct.)

The genus *Vincularia* Defrance is here understood in the sense of the older authors, although this is not correct according to the rules of nomenclature. *Vincularia* is now restricted to those forms which Canu 1907 named *Heterocella.* But *Vincularia fragilis* Defrance 1829 from the Eocene is the type species of the genus of *Vincularia* (cf. Bassler 1953 : 157) and the name *Vincularia* must be reserved for this group. *Heterocella,* therefore, as a synonym of *Vincularia,* must be dropped.

The consequence of this is that there is no name available for the many Cretaceous species of " *Vincularia* " of d'Orbigny, Marsson, Brydone and other authors. Canu (1900) has united most species of *Vincularia* under *Smittipora* Jullien (1881), which Bassler (1953) considered con-generic with *Diplopholeos, Rectonychocella* and *Velumella* Canu & Bassler. But the definition of *Smittipora* does not fit most " *Vincularias* ". Admitted that *Vincularia* has been established primarily as a zoarial growth-form for rod-like stems, there still exists a natural group of forms for which this name has been used and for which another name does not yet exist. On the other hand it seems to be necessary to distinguish the forms which are radicelled or articulated at their base from those which are attached by an encrusting base. This is not the place to give a new classification of *Vincularia,* and it is necessary to retain the old name provisionally.

17. ***Vincularia canalifera*** von Hagenow

(Pl. 5, figs. 7–10 and Pl. 8, figs. 9–12)

1851 *Vincularia canalifera* von Hagenow: 61, pl. 6, fig. 14.
?1851 *Vincularia flexuosa* d'Orbigny: 76, pl. 656, figs. 16–18.
1930 *Vincularia canalifera* von Hagenow; Voigt, 467, pl. 17, fig. 18.

More than thirty fragments of this species were found in the matrix of D.181. They are conspecific with the most common *Vincularia*-species of Maastricht and Kunrade (Netherlands) which was described by von Hagenow as *Vincularia canalifera.* Von Hagenow's figure is not quite typical because the length of the opesia is relatively large, about one third or one quarter of the length of the zooecium. Among some hundred fragments there are only two which correspond to von Hagenow's figure, but this species can show great variation in size and shape of the zooecia and opesiae. The opesia varies between an oval (pl. 5, figs. 7, 9, 10) or more semicircular (pl. 5, fig. 8, pl. 8, figs. 9–11) opening which is truncated more or less proximally. In well preserved specimens it has a slight margin, but never a proximal lip. In the proximal basal region the zooecia are 0·25 mm. long, and when fully developed 0·5 mm.; the length of the opesiae is 0·10–0·17 mm. The avicularia, which have not been figured until now, reach the length of the zooecia or exceed it (pl. 5, fig. 8, pl. 8, figs. 10, 11). They are rare, straight, and appear at the beginning of a new row of zooecia, or are normally enclosed in these. They are broader than the autozooecia and have a flatly rounded prominent distal rim and a small elliptical opesia which is longitudinally oriented. Common to the zooecia and the avicularia is a furrow-like deepening in the median axis of the cryptocyst from which the specific name is derived. Ovicells have never been observed.

The rods have a diameter of 0·5–0·7 mm. and consist of eight to fourteen rows of zooecia. They taper proximally and were articulated or radicelled at their base. This is shown by some of the earliest zooecia which seem to be modified to lodge chitinous rootlets (pl. 5, fig. 7). Their opesiae are smaller and their upper half is covered by a bent calcitic lamella as is seen also in other articulated or radicelled forms.

This species is also common in the Maastrichtian of the Cotentin near Port Filiolet, Fresville and Chef du Pont from which region d'Orbigny described some very similar vincularian species.

I take it that *Vincularia flexuosa* d'Orbigny is conspecific with this species, which is cited by d'Orbigny from Néhou in the Cotentin and from the Santonian of Vendôme. I have studied the type (Nr. 7752 in the d'Orbigny collection) and I cannot find any significant differences. It is figured on pl. 8, fig. 14 for comparison with specimens from Maastricht (pl. 5, figs. 7 and 8 and pl. 8, figs. 11 and 12). The reason why I hesitate to place this species under d'Orbigny's name is, that according to the label the type specimen is from the Santonian of Vendôme (as stated also in his catalogue) although I suspect that it comes from Néhou in the Cotentin. Because it is not clear if the holotype comes from the Cotentin, I prefer the name *Vincularia canalifera* which is given by von Hagenow in the same year as d'Orbigny's name.

Another form from the Cotentin which is very similar to *Vincularia canalifera* is *V. concinna* (d'Orbigny 1851 : 79, pl. 657, figs. 10–12). It may be another synonym. D'Orbigny's holotype is figured on pl. 8, fig. 13; this is the only specimen of this species in the d'Orbigny Collection of Nr. 7756). This specimen, recorded by Canu (1900 : 420) as "insuffisant", has opesiae also which are about 0.11–0.17 mm. long, but the cryptocyst seems to be less deepened than in *Vincularia canalifera* von Hagenow. Unfortunately it shows no avicularia, knowledge of which is very important for the discrimination of many species of *Vincularia* which are very similar and cannot be identified from the work of d'Orbigny. D'Orbigny never figured or mentioned in his species the avicularia, which are rather rare and similar to the autozooecia.

STRATIGRAPHICAL RANGE. Maastrichtian.

SPECIMENS. D.49732. Branched fragment, Upper Maastrichtian, Geulem near Berg, Geul-Valley near Maastricht, Netherlands. Voigt Collection.

D.49733, D.49735–36, D.49737–66. Fragments from the matrix of D.181, Upper Maastrichtian, Cotentin, Manche.

D.49734. Fragment, Upper Maastrichtian Chef du Pont, Cotentin, Manche. Voigt Collection.

D.49840–41. Two fragments, Upper Maastrichtian, St. Pietersberg near Maastricht, Netherlands. Voigt Collection.

D.49842. Fragment, Upper Maastrichtian, St. Pietersberg near Maastricht, Netherlands. Voigt Collection.

Genus *QUADRICELLARIA* d'Orbigny 1850

18. ***Quadricellaria elegans*** d'Orbigny

(Pl. 6, figs. 8–10)

1851 *Quadricellaria elegans* d'Orbigny: 33, pl. 652, figs. 1–5.
1900 *Quadricellaria elegans* d'Orbigny; Canu: 413.
1928 *Quadricellaria excavata* d'Orbigny; Voigt: 112, text-figs. 1–5.
1930 *Quadricellaria excavata* d'Orbigny ; Voigt : 489, pl. 25, figs. 12–14.

Two small fragments of a *Quadricellaria* may be determined as *Q. elegans* d'Orbigny. The size of the opesia compared with the length of the zooecia varies considerably, and Canu may be right in uniting d'Orbigny's three species, *Q. elegans*, *Q. excavata* and *Q. pulchella*, under the name *Q. excavata*, as I did in 1928. My specimens agree largely with the figures of *Q. elegans* d'Orbigny which was first recorded from Néhou (Manche).

This species is represented in my material from Chef du Pont and Port Filiolet. One specimen from Chef du Pont has, on the narrow sides of the segments, two enormous avicularia which are 1 mm. long and have an opesia with a length of 0·3 mm. (pl. 6, fig. 10).

Specimens. D.49591–92. Two worn fragments. From matrix of D.181. Upper Maastrichtian, Cotentin, Manche, France.

A fragment with a large avicularium. Upper Maastrichtian, Chef du Pont, Cotentin, Manche, France. Voigt Collection, Hamburg, Nr. 4133.

Genus *COSCINOPLEURA* Marsson 1887

19. ***Coscinopleura*** sp.

Two minute indeterminable fragments of a *Coscinopleura*, showing only a few zooecia are present. They possibly belong to a species of *Coscinopleura* with small zooecia, like *Coscinopleura lamourouxi* von Hagenow, or to a similar form. Common in the Cotentin Maastrichtian near Port Filiolet and Chef du Pont (Manche).

Specimens. D.49593–94. Two small worn fragments. From the matrix of D.181. Upper Maastrichtian, Cotentin, Manche, France.

Genus *SEMIESCHARINELLA* d'Orbigny 1852[1]

20. ***Semiescharinella complanata*** d'Orbigny

(Pl. 4, figs. 11–15)

1840 *Cellepora ricata* von Hagenow: 616.
1852 *Semiescharinella complanata* d'Orbigny: 427, pl. 714, figs. 1–4.

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[1] D'Orbigny published his genera *Semiescharinella* and *Repteschárinella* on p. 427 and p. 428 of his work. According to Sherborn (*Geol. Mag.* 1889 : 223–225) pages 187–472 appeared in 1852. I follow here the dates given by Sherborn, although Lang (1917 : 172) states 1853 for *Repteschárinella* and d'Orbigny himself writes 1851 for both genera.

1852 *Escharinella simplex* d'Orbigny: 205, pl. 683, figs. 14–16.
1900 *Rhagasostoma simplex* (d'Orbigny); Canu: 433.
1930 *Micropora subgranulata* (von Hagenow) Voigt (pars): 476, pl. 24, fig. 18 (non 19).
1959 *Semiescharinella complanata* (d'Orbigny) Voigt: 54, pl. 6, fig. 1.
1962 *Semiescharinella complanata* (d'Orbigny) Berthelsen: 134, pl. 14, figs. 2–3.

Two very small unilaminar fragments agree very well with some specimens from Chef du Pont and with d'Orbigny's type-specimen from Sainte Colombe (Manche). The size of the zooecia is a little less in the type-specimen (about 0·56–0·60 mm.) compared with 0·70 mm. in D.49595–96; but the abundant material in the author's collection shows that the size of the zooecia and opesiae is highly variable in this species. The " TYPE " is a fragment, with *c.* 18 zooecia, in which the relative length and width of the zooecia differ from d'Orbigny's figure as noted by Canu (1900 : 421), although in the catalogue of the d'Orbigny Collection only one specimen from Sainte Colombe (Manche) is registered. The bilaminar *Escharinella simplex* d'Orbigny from Néhou (Manche) belongs to the same species. The distal pore which was interpreted by Canu as the trace of the ovicell is a true avicularium. Nevertheless, there are some real ovicells which are developed in place of the avicularia (see pl. 4, fig. 15).

Comparison of the photographs (pl. 4, figs. 13–15) shows that there is no variation in the shape or size of the zooecia, nor of the opesiae, nor amongst the distal avicularia. I have figured the only poor fragment from the d'Orbigny collection which must be regarded as the type specimen (pl. 4, fig. 15). This species is congeneric with *Cellepora* (*Discopora*) *subgranulata* von Hagenow (1851 : 91, pl. 11, fig. 15) which was chosen by Lang (1917 : 172) as the type species for the genus *Reptescharinella* d'Orbigny 1852. D'Orbigny had united under this name eight Cretaceous, one Tertiary and two Recent species, of quite distinct systematic differences, said to be characterized by an " ouverture mediocre ", a " pore spécial " and encrusting zoaria. The genus *Semiescharinella* was not discussed by Lang, being represented only by *Semiescharinella complanata* d'Orbigny. There is no doubt what d'Orbigny meant by this name, and I prefer it, proposing to drop *Reptescharinella* as a synonym of *Semiescharinella*, the mode of growth being no generic criterion. This form was first described by von Hagenow 1840 under the name *Cellepora ricata* without any figure (Voigt 1959 : 54).

Stratigraphical range. Maastrichtian-Danian.

Specimens. D.49595–96. Two small worn fragments. From the matrix of D.181. Upper Maastrichtian, Cotentin, Manche, France.

D.49847. A small fragment. Upper Maastrichtian, Chef du Pont, Cotentin, Manche, France. Voigt Collection.

A small fragment showing an ovicelled zooecium. Upper Maastrichtian, Chef du Pont, Cotentin, Manche, France. Voigt Collection Hamburg Nr. 3918b.

Bilaminar fragment, Holotype of *Escharinella simplex* d'Orbigny. Upper Maastrichtian, Néhou, Cotentin, Manche, France. d'Orbigny Collection, Paris, Musée d'Histoire Naturelle Nr. 7942.

Genus ***ROSSELIANA*** Jullien 1888

21. ***Rosseliana thomasi*** sp. n.

(Pl. 1 fig. 6, and Pl. 4, figs. 4–6)

TYPE SPECIMEN. D.49597. Zoarium encrusting a branched fragment of *Radulopora minor* n. g. n. sp. Upper Maastrichtian, Chef du Pont, Cotentin, Manche, France. Collection E. Voigt.

DERIVATIO NOMINIS. In honour of Dr. Dighton Thomas, London, who first detected this species in the matrix of *Castanopora jurassica* (Gregory).

DIAGNOSIS. A *Rosseliana* with encrusting zoarium. Zooecia very small, oval, only 0·33 mm. long, with smooth cryptocyst and sharply raised rim in the distal region of the zooecia. Opesiae semicircular, occupying nearly a third of the length of the zooecia, sometimes with very inconspicuous lateral processes, but never trifoliate in shape; its lower rim is straight without opesiules. Ovicells globular swellings above the opesia and occupying the proximal part of the distal zooecium.

DESCRIPTION. In addition to the British Museum specimen, which encrusts a branch of *Multicrescis laxata* d'Orbigny, there are two others from Chef du Pont (Manche). They show, although they are more fragile, the same essential specific characters, having no avicularia and no trifoliate opesiae. In some zooecia, very minute lateral processes might indicate a *Floridina*-like opesia, but this is so negligible that it can be ignored. They are therefore classified as *Rosseliana* and not *Floridina* or *Floridinella*. Nevertheless, it is clear that the difference between *Rosseliana* and *Floridinella*, based only on the existence of broad opesiular indentations in the latter, is slight. The specimens are very similar to that figured by Bassler (1953, fig. 130.4), but he only records *Rosseliana* from the Oligocene to Recent.

There are very few species with which this form could be compared. The shape and size of zooecia are very similar in *Floridina* (or better *Floridinella*) *scutata* Levinsen (1925 : 345, pl. 4, fig. 39) from the Danish Maastrichtian Chalk and Danian, and *Semieschara complanata* d'Orbigny (1852 : 369, pl. 708, figs. 5–8). Apart from the free unilaminar fronds of the latter, it is very difficult to find any constant difference between these two forms, which are distinguished from our new *Rosseliana thomasi* only by their opesiae, always markedly trifoliate as in *Floridina* or *Floridinella*. Pl. 4, fig. 7, shows a specimen of *Floridinella scutata* Levinsen from a Maastrichtian flint drift boulder from northern Germany. The difference of this species from *Rosseliana thomasi* n. sp. is clearly seen in the opesia which has significant lateral indentations.

STRATIGRAPHICAL RANGE. Upper Maastrichtian.

SPECIMENS. D.47323. Encrusting zoarium with some ovicelled zooecia on *Multicrescis laxata* d'Orbigny (= D.49575). In the matrix of *Castanopora jurassica* (Gregory) (D.180) Upper Maastrichtian, Cotentin, Manche, France.

Zoarium encrusting an echinoid fragment. Upper Maastrichtian, Port Filiolet, Cotentin, Manche, France. Voigt Collection, Hamburg, Nr. 3932.

Genus ***MICROPORA*** Gray 1848 (non Eichwald 1855)

22. ***Micropora transversa*** (d'Orbigny)

(Pl. 7, figs. 9–12)

1851 *Vincularia transversa* d'Orbigny: 78, pl. 657, figs. 7–9.
1887 *Vincularia rugica* Marsson: 65, pl. 6, fig. 8.
1930 *Micropora rugica* (Marsson) Voigt: 472, pl. 21, fig. 20.
1951 *Micropora rugica* (Marsson) Voigt: 63, pl. 9, fig. 10 and pl. 10, fig. 4.

HOLOTYPE. Two minute fragments evidently 2 pieces of one specimen. Upper Maastrichtian, Néhou, Cotentin, Manche, France. d'Orbigny Collection, Paris, Musée d'Histoire Naturelle Nr. 7755.

There is only a very small fragment corresponding to the length of a single zooecium of this species in the matrix of D.181. The two symmetrical opesiules below the opesia show clearly that it must belong to *Vincularia transversa* d'Orbigny, the type of which, from Néhou, (pl. 7, figs. 10–11) was studied by the author. There is only one poorly preserved fragment in d'Orbigny's collection which is recorded in his catalogue. It is now broken into two pieces. It does not correspond to d'Orbigny's figure and description, because the paired opesiules, which are clearly visible, are neither mentioned in his text nor figured in his drawing; they seem to be indicated by the deep furrows accompanying the thick margin of the zooecia, but they do not correspond to what d'Orbigny called " une dépression lanceolée " which is situated below the aperture. This depression must correspond to the lanceolate cryptocyst of d'Orbigny's figure. I found some well preserved fragments at Port Filiolet and Chef du Pont (Cotentin), see pl. 7, fig. 12.

This form is conspecific with Marsson's *Vincularia rugica* as is proved by many specimens from the Maastrichtian Chalk of Rügen and other localities in northern Germany. Marsson who published the first good description and figure of this species, was therefore unable to recognize that his species was the same as d'Orbigny's, and it is understandable that, since Marsson's description, this form has been recorded only under the name *rugica*. Another similar species is *Vincularia undata* d'Orbigny from the Santonian of Vendôme, which also has true opesiules below the opesia, not indicated in d'Orbigny's figure (d'Orbigny 1851 : 75, pl. 656, figs. 10–12) but which can be seen on the holotype.

The appearance of *Micropora transversa* can vary considerably as shown in Voigt's figures (1951). The diameter of the rods is from 0·5–0·7 mm., and the number of zooecial rows varies between five and ten. The length of the normal zooecia is 0·49–0·54 mm. The basal attenuated part of some rods shows clearly that this species was articulated or radicelled (cellariform). This means that this form is not congeneric with all true *Micropora*, and it could be suggested that it belongs to a new genus. But I hesitate to erect a new genus for it because it is not impossible that this form is conspecific with *Dimorphostylus tetrastichus* Voigt 1928. The genus *Dimorphostylus* was established for articulated rods, in which the zooecia are only developed on one side. But the size and other features of the zooecia in *Micropora rugica* and in *Dimorphostylus tetrastichus*, which are often associated together in the same localities, are identical, and there is the suspicion that *Dimorphostylus tetrastichus* might represent specimens with the zooecia developed only on one side, and that the differentiation in a frontal and reversed side may be pathological. The two forms have not yet been found united in one specimen, but if they were, the generic name *Dimorphostylus* must be applied to *Micropora transversa* d'Orbigny. Therefore it is provisionally here referred to *Micropora*, which also indicates that it may belong to the Microporidae.

STRATIGRAPHICAL RANGE. Maastrichtian; Lower Maastrichtian of Rügen and Denmark and Upper Maastrichtian of the Cotentin (Manche), Maastricht and Ilten near Hanover.

SPECIMENS. D.49768. A minute fragment. From matrix of D.181. Upper Maastrichtian, Cotentin, Manche, France.

D.49769. A well preserved fragment. Upper Maastrichtian, Chef du Pont, Cotentin, Manche, France. Voigt Collection.

Genus ***PUNCTURIELLA*** Levinsen 1925

23. ***Puncturiella*** cf. ***superba*** Brydone

(Pl. 4, figs. 8–10)

1936 *Puncturiella superba* Brydone: 84, pl. 40, fig. 18.

The small unilaminar fragment with about a dozen poorly preserved zooecia, shows the cryptocyst pierced by two outer and two inner rows of pores. These are barely visible because they are partly obscured by recrystallization of the calcite, and the distal avicularium which is directed obliquely is very obscure. However the identity of this specimen with a few unilaminar fragments from Fresville and Chef du Pont is evident (pl. 4, figs. 8–9), and they are probably identical with some very similar specimens from Maastricht which are free or encrusting, but whose dimensions are a little larger.

The average length of zooecia from the Cotentin localities is about 0·65–0·70 mm., that from Maastricht 0·80–1·00 mm., although some zooecia from the two localities are the same size, and it may be that the difference is ecological. The only form with which D.49598 can be identified is *Puncturiella superba* Brydone from the Lower Maastrichtian Chalk of Trimingham (Norfolk), in which the zooecia are about 0.65–1 mm. long.

STRATIGRAPHICAL RANGE. Maastrichtian.

SPECIMENS. D.49598. A small worn fragment embedded in matrix of D.181. Upper Maastrichtian, Cotentin, Manche, France.

D.49599. A small fragment. Upper Maastrichtian, Chef du Pont, Cotentin, Manche, France. Voigt Collection.

D.49600. A small well preserved fragment in matrix. Upper Maastrichtian Md, St. Pietersberg near Maastricht. Voigt Collection.

Genus *LUNULITES* Lamarck

24. ***Lunulites*** sp.

One very small fragment which is worn and shows a few zooecia is indeterminable. It seems to be conspecific with one of the numerous species of *Lunulites* represented in the Maastrichtian of the Cotentin.

SPECIMENS. D.49601. A very small indeterminable fragment. In matrix of D.181. Upper Maastrichtian, Cotentin, Manche, France.

Genus *ONYCHOCELLA* Jullien 1881

25. ***Onychocella nysti*** (von Hagenow)

(Pl. 6, figs. 3–4)

1851 *Eschara nysti* von Hagenow: 78, pl. 9, figs. 15–17.
1930 *Onychocella nysti* (von Hagenow) Voigt: 459, pl. 16, figs. 14–16.

One small fragment belongs to this species which is very common at all European Maastrichtian localities and which I found at Port Filiolet and Chef du Pont (Manche). It has not previously been recorded from the Cotentin Maastrichtian.

STRATIGRAPHICAL RANGE. Campanian-Maastrichtian.

SPECIMENS. D.49602. A worn fragment. From the matrix of D.181. Upper Maastrichtian. Cotentin, Manche, France.

D.49603. A well preserved fragment. Upper Maastrichtian, Chef du Pont, Cotentin, Manche, France. Voigt Collection.

26. ***Onychocella*** cf. ***cepha*** (d'Orbigny)

(Pl. 6, figs. 1–2)

1851 *Eschara cepha* d'Orbigny: 143, pl. 670, figs. 8–10.

Two fragments of a narrow *Onychocella* belong to a species which is very abundant near Chef du Pont (Manche) and which is not distinguishable from an *Onychocella* from the Maastrichtian of Archiac (Gironde). Of the numerous species of *Onychocella* described by d'Orbigny from the French Cretaceous, the only one which can be compared with this form is *Eschara cepha* d'Orbigny from Royan, although the type-specimen has more slender zooecia and thinner rims surrounding the zooecia. Comparison with the type alone would suggest a different species, but when compared with all the material from Archiac and Chef du Pont, these differences are much diminished and identity is more justified than the foundation of a new species.

STRATIGRAPHICAL RANGE. Maastrichtian.

MEASUREMENTS.

$L_z = 0{\cdot}48\text{–}0{\cdot}55$ mm.
$l_z = 0{\cdot}30\text{–}0{\cdot}37$ mm.
$h_o = 0{\cdot}10\text{–}0{\cdot}17$ mm.
$l_o = 0{\cdot}10\text{–}0{\cdot}13$ mm.
$L_{av} = 0{\cdot}70\text{–}0{\cdot}75$ mm.

SPECIMENS. D.49604. A branched fragment. From the matrix of D.181. Upper Maastrichtian, Cotentin, Manche, France.

D.49605. A small fragment. From the matrix of D.181. Upper Maastrichtian, Cotentin, Manche, France.

D.49606. A fragment. Upper Maastrichtian, Chef du Pont, Cotentin, Manche, France. Voigt Collection.

27. *Onychocella bellona* (d'Orbigny)

(Pl. 6, figs. 5–7)

1851 *Eschara bellona* d'Orbigny: 134, pl. 668, figs. 7–9.
1900 *Rhagasostoma bellona* (d'Orbigny) Canu (pars): 431.

Two fragments of this broad bilaminar species agree in all details with the material collected by the author at Chef du Pont (Manche) and with as pecimen in d'Orbigny's collection from Néhou (Manche). (d'Orbigny Collection Nr. 7812.)

The small difference between the diameter of the apertures in our figured specimen and that of d'Orbigny is irrelevant because it is also shown in the specimens from Chef du Pont. The opesiae of the fertile zooecia are a little longer than the others. This species belongs to the group of *Onychocella lamarcki* von Hagenow, which is closely allied to it; but the latter always shows more slender branches (1·2–2·0 mm. diameter), and shorter and thicker zooecia, and the difference in size of the fertile and non fertile zooecia is much more evident than in *Onychocella bellona* d'Orbigny.

It is the same with the fertile zooecia of *Onychocella lamarcki* von Hagenow from Maastricht, but the zoaria of that species are always flat and lamellar.

MEASUREMENTS.

$L_z = 0{\cdot}60\text{–}0{\cdot}70$ mm.
$l_z = 0{\cdot}33\text{–}0{\cdot}45$ mm.
$h_o = 0{\cdot}12\text{–}0{\cdot}18$ mm.
$l_o = 0{\cdot}12\text{–}0{\cdot}19$ mm.
$L_{av} = 0{\cdot}75\text{–}1{\cdot}00$ mm.
$l_{av} = 0{\cdot}22\text{–}0{\cdot}27$ mm.

This species has been found only in the Cotentin Maastrichtian.

STRATIGRAPHICAL RANGE. Upper Maastrichtian.

SPECIMENS. D.49607. A worn fragment. From the matrix of D.181. Upper Maastrichtian, Cotentin, Manche, France.

D.49608. A well preserved fragment. Upper Maastrichtian, Chef du Pont, Cotentin, Manche, France. Voigt Collection.

A well preserved fragment with ovicelled zooecia. Upper Maastrichtian, Néhou, Cotentin, France. d'Orbigny Collection, Paris, Musée d'Histoire Naturelle Nr. 7812.

Genus ***ONYCHOCELLARIA*** Voigt 1957

28. ***Onychocellaria caecilia*** (d'Orbigny)

(Pl. 5, figs. 1–6)

1851 *Eschara caecilia* (d'Orbigny): 138, pl. 669, figs. 4–7.

The zoarium was cellariiform in growth. This is proved by the tapering proximal ends of the segments and by pits occasionally found on the cryptocyst in which rootlets are inserted. This criterion, combined with the straight avicularia, puts it in the genus *Onychocellaria*, although the endozooecial ovicell, which is characteristic for this genus, has not yet been observed.

The zooecia, the length of which is 0·4–0·5 mm., are nearly rectangular and are very often distinguished by a small horizontal band above the distal rim of the opesia. The slit-like pit between the opesia and this band is very characteristic, and is shown in d'Orbigny's figures. The opesiae, which vary greatly in size, may be rounded or oval to high-semicircular. In some segments the whole opesia or its upper half is closed by a calcareous lamella.

Measurements.

L_z = 0·42–0·51 mm.
l_z = 0·20–0·25 mm.
h_o = 0·10–0·70 mm.
l_o = 0·10–0·11 mm.
L_{Av} = 0·55–0·58 mm.
l_{Av} = 0·25–0·30 mm.

This species is represented by many small fragments. It is characteristic of the Maastrichtian of the Cotentin, and has also been found in abundance by the present author near Port Filiolet (Manche). The specimens agree entirely with the original specimens of d'Orbigny from the Maastrichtian of Néhou. These are not " usé " as stated by Canu (1900 : 420).

Stratigraphical range. Upper Maastrichtian.

Specimens. D.49726. A small fragment with avicularia. From the matrix of D.181. Upper Maastrichtian, Cotentin, Manche, France.

D.49727. Another fragment with avicularium. From the matrix of D.181. Upper Maastrichtian, Cotentin, Manche, France.

D.49728–29. Two worn fragments. From the matrix of D.181. Upper Maastrichtian, Cotentin, Manche, France.

D.49767. A small fragment corresponding in preservation to D.49730. From the matrix of D.181. Upper Maastrichtian, Cotentin, Manche, France.

D.49849–54. 6 fragments from the matrix of D.181. Upper Maastrichtian, Cotentin, Manche, France.

D.49848. Eight very worn small fragments from the matrix of D.181. Locality and horizon as above.

D.49730. A well preserved fragment with some avicularia. Upper Maastrichtian, Chef du Pont, Cotentin, Manche, France. Voigt Collection.

D.49731. A well preserved fragment. Upper Maastrichtian, Chef du Pont, Cotentin, Manche, France. Voigt Collection.

Genus ***PLIOPHLOEA*** Gabb & Horn 1862

29. ***Pliophloea*** sp.

(Pl. 7, fig. 3)

Of this species there is but one encrusting young zoarium, which is composed of the ancestrula and a dozen zooecia. The ancestrula is 0·20 mm. long and the other zooecia have a length up to 0·50 mm. The smooth intraterminal front wall shows about twelve to thirteen costae which are barely visible. The orifice is cribriline to slightly pliophloean according to Lang's definition. There is only one avicularium—if the interpretation as avicularium is correct—which is *c.* 0·20 mm. long and which is close to the ovicelled zooecium on the right of our figure. Details of the spines are not visible. *Pliophloea gluma* Lang (1921 : 188, pl. 6, fig. 3) from the Danian shows some affinities in the shape of the zooecia and the apertures, but has clearly distinct costae, and visible intercostal fusions, and the zooecia are only 0·40 mm. long. There is no other species hitherto described with which this form can be identified and therefore it may be supposed that it is a new one. But this one poor specimen does not suffice to found a new species.

STRATIGRAPHICAL RANGE. This form has not previously been observed in the Maastrichtian of the Cotentin.

SPECIMENS. D.47324. Small encrusting zoarium with ancestrula and an ovicelled zooecium. In the matrix of *Castanopora jurassica* (Gregory) D.180. Upper Maastrichtian, Cotentin, Manche, France.

Genus ***DECURTARIA*** Jullien 1886
(= ***Prosoporella*** Marsson 1887)

30. ***Decurtaria*** cf. ***cornuta*** (Beissel)

(Pl. 7, figs. 1–2)

1865 *Semiescharipora cornuta* Beissel: 58, pl. 7, figs. 77–81.
1887 *Prosoporella cornuta* Marsson: 100.
1922 *Decurtaria cornuta* (Beissel) Lang: 388, text-fig. 124, pl. 8, fig. 9.
1925 *Barroisina trifossata* Levinsen: 387, pl. 8, fig. 6.
1930 *Decurtaria cornuta* (Beissel) Voigt: 516, pl. 32, fig. 6.

This species is represented by a fairly large zoarium composed of about thirty zooecia. Unfortunately it is covered by a film of minute calcite-crystals which hides many of the characteristic minute details of the costae and the orifices. The small number of costae (six to seven) and the very stout distal shield indicate it to be *Decurtaria cornuta*, although the shape of the orifice is more like that of *Decurtaria allecta* Lang (1922 : 386, pl. 8, fig. 8) from the Upper Maastrichtian of Maastricht. D.49609 corresponds exactly to a fragment from Chef du Pont (Manche). In some respects that form might be regarded as intermediate between the two species, which are, indeed, more alike than is stated by Lang who had only one specimen of his *D. allecta* from Maastricht. *Decurtaria cornuta* is not confined to the Lower Maastrichtian as might be concluded from Lang's work. I found a small but typical fragment of this species in the Upper Maastrichtian of Biebosch (South Limburg, Netherlands).

It seems that the shape of the orifice is not so constant as was assumed by Lang. According to him, in *D. cornuta* the orifice should be " super-cribriline " and in *D. allecta* " supernormal ". But Beissel had already stated that the different types of orifice shape may be observed in the same zoarium, and he has figured both forms in his figs. 77 and 78. The size of the zooecia is between 0·57 and 0·65 mm. *Barroisina trifossata* Levinsen is a synonym of this species which I concluded from the examination of Levinsen's type specimen.

Stratigraphical range. Maastrichtian.

Specimens. D.49609. A complete zoarium with ancestrula and some ovicelled zooecia. From the matrix of D.181. Upper Maastrichtian, Cotentin, Manche, France.

An incomplete zoarium. Upper Maastrichtian, Chef du Pont, Cotentin, Manche, France. Voigt Collection, Hamburg, Nr. 4137.

Genus ***FRURIONELLA*** Canu & Bassler 1926

30. ***Frurionella fertilis*** sp. n.

(Pl. 8, figs. 5–7)

Holotype. D.49610. Upper Maastrichtian, Chef du Pont, Cotentin, Manche, France. Collection E. Voigt.

Derivatio nominis. Derived from fertilis = generative, on account of the numerous ovicells.

Diagnosis. A slender species of *Frurionella*, with bilaminar branches consisting of three to four alternating rows of zooecia. Zooecia not distinct, small, with quadrangular to high triangular or semicircular opesiae whose proximal margin is straight and generally provided with an inconspicuous proximal lip caused by the swelling of the median avicularium below the opesia. Elliptical or linear indistinct pores which may be avicularia are developed in the median axis of the zooecium. Ovicells numerous, forming deep characteristic cavities above the apertures if the covering lamina has been destroyed.

MEASUREMENTS.

$L_z = 0{\cdot}50\text{–}0{\cdot}62$ mm.
$h_0 = 0{\cdot}10\text{–}0{\cdot}12$ mm.
$l_0 = 0{\cdot}10\text{–}0{\cdot}12$ mm.

REMARKS. A small fragment, showing a scarcely constricted opesia with a minute avicularium below it, has been recognized as belonging to this new species which is represented from Chef du Pont by two other similar specimens. This form cannot be identified with any of the few known species of *Frurionella*. It is smaller in its zoarial and zooecial dimensions than the other species of this genus. At first it was supposed that it might be the slender distal branch of another new species of *Frurionella* which is much larger and very common at Fresville (Cotentin, Manche). This is improbable because there are no intermediate stages between these two very different forms and no distal branches smaller than 2–1·5 mm. seem to exist in the second species. This other species of *Frurionella* from Fresville (pl. 8, fig. 8) is conspecific with *Frurionella europaea* Voigt (1951 : 60, pl. 9, figs. 1–3) from the Upper Maastrichtian of Ilten (Hannover) and Kunrade (Netherlands). It has now also been found at Maastricht (Netherlands).

STRATIGRAPHICAL RANGE. Maastrichtian.

SPECIMENS. D.49610. Holotype see above.

D.49611. A small worn fragment in matrix. From the matrix of D.181. Upper Maastrichtian, Cotentin, Manche, France.

D.49612. A fragment with broken ovicelled zooecia. Horizon and locality as above.

Genus ***BEISSELINA*** Canu 1913

32. ***Beisselina striata*** (Goldfuss)

(Pl. 8, figs. 3–4)

1826 *Eschara striata* Goldfuss: 25, pl. 8, fig. 16.
1960 *Beisselina striata* (Goldfuss) Wiesemann: 27, pl. 1, figs. 1–3, pl. 2, figs. 3–4; pl. 12, figs 3–4; text-figs. 3e, 4 9–10; 5, Nrs. 12–13 (with additional synonymy).
1967 *Beisselina striata* (Goldfuss) Voigt: 72, pl. 25, fig. 1.

One specimen belongs to this common Maastrichtian species which is, according to Wiesemann, represented near Chef du Pont (Manche). Nevertheless the diameter of the stem (1·5 mm.) and the orifices (peristomicia) are a little smaller (0·08–0·12 mm.) than in most specimens from the type locality of Maastricht, and Kunrade, although the length of the zooecia (distance between proximal and distal apertures) is the same. Specimens with such small orifices are not lacking, and all intermediate sizes occur at these localities, but they are rare. For comparison see pl. 8, fig. 4, showing the surface of a worn specimen from Maastricht itself. These small forms are more common in the " Tuffeau de St. Symphorien " in the Basin of Mons (Belgium.)

Stratigraphical range. Maastrichtian.

Specimens. D.49721. A worn fragment. From the matrix of D.181. Upper Maastrichtian, Cotentin, Manche, France.

D.49722. A worn fragment. Upper Maastrichtian, Geulem, near Berg, Geul valley near Maastricht (Netherlands). Voigt Collection.

Genus ***BEISSELINOPSIS*** Voigt 1951

33. ***Beisselinopsis flabellata*** (d'Orbigny)

(Pl. 8, figs. 1–2)

1852 *Escharifora flabellata* d'Orbigny: 460, pl. 715, figs. 10–12.
non 1930 *Beisselina flabellata* (d'Orbigny) Voigt: 525, pl. 34, fig. 11.

One incomplete young zoarium represents d'Orbigny's species which is common at Sainte Colombe (Manche) and the type of which from this locality was studied by the present author. There are some specimens from Chef du Pont (Manche) which agree very well with *Beisselinopsis flabellata* d'Orbigny although they are more elongate than the flabelliform zoarium of d'Orbigny's type specimen. The species identified as *Porina flabellata* (d'Orbigny) by Marsson (1887 : 85) is *Beisselinopsis marginata* v. Hagenow 1839 (cf. Voigt 1959 : 11, pl. 9, figs. 1–2). The similar Danian and Montian form determined as *Porina* or *Beisselina flabellata* (d'Orbigny) by Levinsen (1925, pl. 7, fig. 83) and Voigt (1930 partim : 525, pl. 34, fig. 11) is neither conspecific nor congeneric and corresponds to *Eschara oblita* Kade (1852 : 29, pl. 1, fig. 18) as stated by Berthelsen (1962 : 201, pl. 24, fig. 6) and Voigt (1964 : 458, pl. 8, fig. 8 and pl. 14, figs. 1–3) and belongs to the genus *Pavobeisselina* Voigt 1964. It was formerly assigned to *Beisselinopsis* Voigt 1951, but this attribution was incorrect because *Beisselinopsis* has no ascopore which can always be observed in *Pavobeisselina*. The inner structure of *Beisselinopsis flabellata* d'Orbigny does not show any ascopore in the frontal wall as is always the case in *Beisselina* and flabelliform *Pavobeisselina*. Therefore it must be regarded as a true *Beisselinopsis*.

Stratigraphical range. Upper Maastrichtian.

Specimens. D.49723. A young zoarium. From the matrix of D.181. Upper Maastrichtian, Cotentin, Manche, France.

An adult zoarium. Upper Maastrichtian, Chef du Pont, Cotentin, Manche, France. Voigt Collection, Hamburg, Nr. 3908.

II. BRACHIOPODA

Genus ***THECIDEA*** Defrance 1832

Thecidea papillata (von Schlottheim)

(Pl. 1, figs. 9–10)

1959 *Thecidea papillata* von Schlotheim; Backhaus: 21, pl. 1, figs. 1–4 (see for all references).

TABLE I.

List of the species from the matrix of "*Castanopora*" *jurassica* (Gregory) (D.180) and *Onychocella piriformis* (Goldfuss) (=*Onychocella bathonica* (Gregory) (D.181).

			Maastrichtian localities of the Cotentin (Manche)					
I. POLYZOA	In block with D.180	In block with D.181	Sainte-Colombe*	Néhou*	Fresville	Port Filiolet	Chef du Pont	Maastrichtian of Maastricht
1. *Berenicea* sp.		+			+			
2. *Entalophora benedeniana* (von Hagenow) 1851		+					+	+
3. *Idmidronea macilenta* (von Hagenow) 1851		+	+		+			+
4. *Heterocrisina communis* (d'Orbigny) 1853		+	+		+	+	+	+
5. *Crisisina carinata* (Roemer) 1840		+	+		+	+	+	+
6. *Osculipora truncata* (Goldfuss) 1826		+			+		+	+
7. *Reteporidea lichenoides* (Goldfuss) 1826		+				+	+	+
8. *Petalopora* sp.		+				+	+	
9. *Multicrescis laxata* (d'Orbigny) 1854	+		+					
10. *Membranipora unipora* (Marsson)		+	+			+		
11. *Amphiblestrella elegans* von (Hagenow) 1851		+			+	+		+
12. *Radulopora minor* n. sp.		+				+	+	+
13. *Hagenowinella* cf. *incrassata* (d'Orbigny) 1853		+	+		+			
14. *Bactrellaria rugica* Marsson 1887		+				+	+	+
15. *Stamenocella marginata* (d'Orbigny) 1852		+	+				+	
16. *Thyracella* cf. *meudonensis* d'Orbigny 1851		+				+	+	
17. *Vincularia canalifera* von Hagenow 1851		+		+	+	+	+	+
18. *Quadricellaria elegans* (d'Orbigny) 1951		+				+	+	+
19. *Coscinopleura* sp.		+					+	
20. *Semiescharinella complanata* d'Orbigny 1852		+	+				+	
21. *Rosseliana thomasi* n. sp.	+	+				+	+	
22. *Micropora transversa* (d'Orbigny) 1851		+		+		+	+	
23. *Puncturiella* cf. *superba* Brydone 1936		+			+		+	+
24. *Lunulites* sp.		+					+	
25. *Onychocella nysti* (von Hagenow) 1851		+				+	+	+
26. *Onychocella* cf. *cepha* (d'Orbigny) 1851		+	+			+	+	
27. *Onychocella bellona* (d'Orbigny) 1851		+	+	+		+	+	
28. *Onychocellaria caecilia* (d'Orbigny) 1851		+		+			+	
29. *Pliophloea* sp.	+							
30. *Decurtaria* cf. *cornuta* (Beissel) 1865		+					+	
31. *Frurionella fertilis* n. sp.		+					+	
32. *Beisselina striata* (Goldfuss) 1926		+				+	+	+
33. *Beisselinopsis flabellata* (d'Orbigny) 1852		+	+			+	+	
II. BRACHIOPODA								
34. *Thecidea papillata* (von Schlottheim) 1813		+		+	+	+	+	+

* After d'Orbigny.

Two small valves of this very common and characteristic brachiopod of the " Craie à Thecidées " were found in the matrix of D.181. They are indistinguishable from those of the Cotentin Maastrichtian collected by the author. The collection of the " Geologisches Staatsinstitut " Hamburg possesses about 850 specimens from Chef du Pont, Fresville and Port Filiolet, which were studied in the monograph by Backhaus. The locality " Port Fiolet " (Backhaus 1959 : 27 and Hofker 1959 : 369, 380, 381) should be " Port Filiolet ".

STRATIGRAPHICAL RANGE. Maastrichtian, mainly Upper Maastrichtian.

SPECIMENS. BB.42981. Pedicle valve. From the matrix of D.181. Upper Maastrichtian, Craie à Thecidées, Cotentin, Manche, France.

BB.42982. Small dorsal valve. Horizon and locality as above.

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EXPLANATION OF PLATES

Some of the specimens of Bryozoa and Brachiopoda referred to and figured in this publication are housed in the collections of the British Museum (Natural History) and are prefixed by the letters D and BB respectively.

PLATE 1

Petalopora sp. (p. 18)

Fig. 1. Worn branch with narrow ribs between the small mesopores. From the matrix of D.181, Upper Maastrichtian (Cotentin, Manche). ×25. D.49573.

Fig. 2. Branch in similar condition to fig. 1 with larger mesopores and peristomes. Upper Maastrichtian, Port Filiolet (Cotentin, Manche). Presented by the author. ×25. D.49574.

Fig. 3. Well preserved branch. Upper Maastrichtian, Chef du Pont (Cotentin, Manche). ×25. Voigt Collection, Hamburg, Nr. 3969.

Crisisina carinata (Roemer) (p. 17)

Fig. 4. Worn fragment with damaged peristomes, lateral view. From the matrix of D.181 Upper Maastrichtian (Cotentin, Manche). ×25. D.49566.

Fig. 5. Worn fragment, frontal view. Upper Maastrichtian, Port Filiolet (Cotentin, Manche). Presented by the author. ×25. D.49567.

Multicrescis laxata d'Orbigny (p. 18) (See also pl. 4 figs. 4–6)

Fig. 6. Worn fragment D.49575 with encrusting *Rosseliana thomasi* n. sp. (D.47323) in matrix of *Castanopora jurassica* (Gregory) (D.180). Upper Maastrichtian (Cotentin, Manche). ×20.

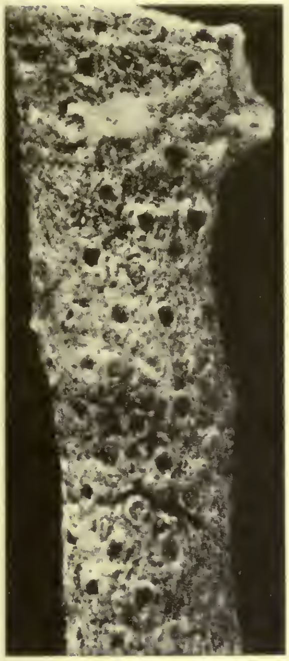
Fig. 7. Holotype. Upper Maastrichtian, Sainte Colombe (Cotentin, Manche) in coll. d'Orbigny Nr. 8416, Musée d'Histoire Naturelle, Paris. ×12.

Fig. 8. Holotype. ×25.

Thecidea papillata von Schlottheim (p. 40)

Fig. 9. Pedicle (ventral) valve with growth-facet on the apex, with the cast of a small lamellibranch on the right. From the matrix of D.181. Upper Maastrichtian (Cotentin, Manche), attesting the origin from the " Craie à Thecidées " of the Cotentin-region. *c.* ×12. BB.42981.

Fig. 10. Small dorsal valve slightly damaged. From the matrix of D.181. *c.* ×12. BB.42982.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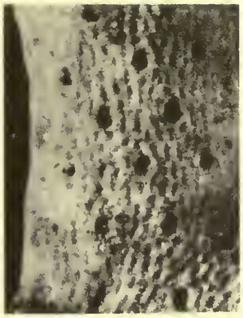
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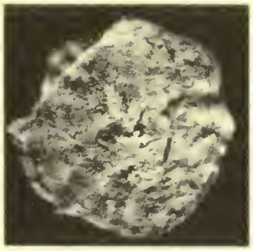
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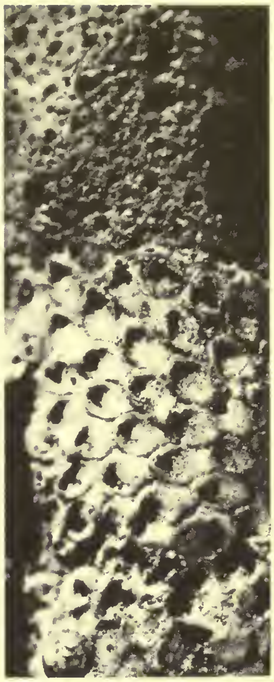
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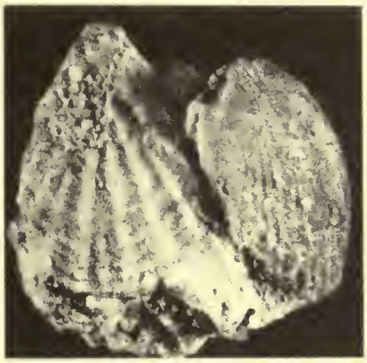
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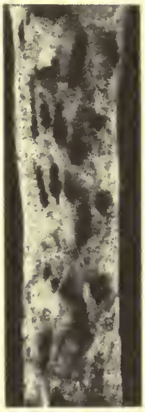
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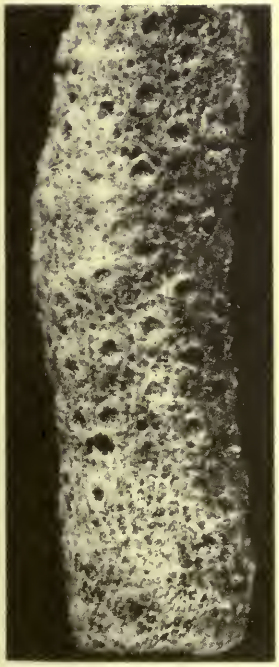
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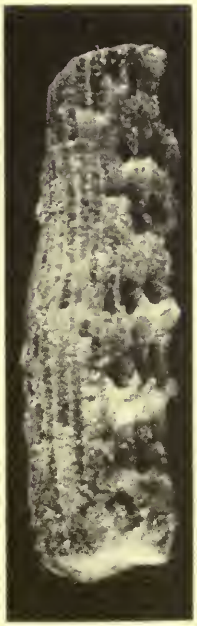
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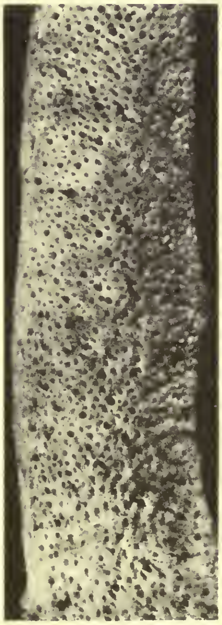
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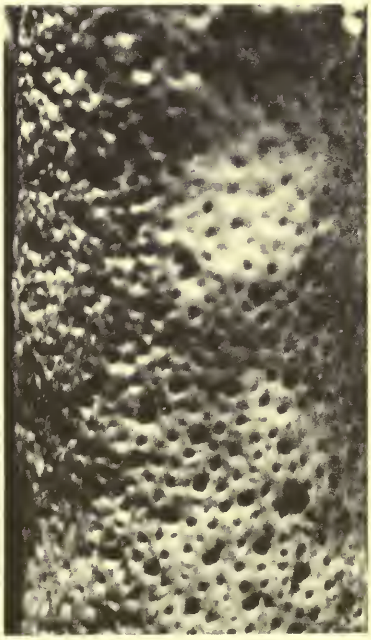
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PLATE 2

***Hagenowinella* cf. *incrassata* (d'Orbigny) (p. 23)**

FIG. 1. Part of the encrusting zoarium showing an avicularium in the left upper corner and some damaged zooecia in the proximal region. From the matrix of D. 181. Upper Maastrichtian (Cotentin, Manche). × 20. D. 49583.

FIG. 2. Worn specimen with broken ovicells. The deeply immersed horseshoe-like processes in the interior of the zooecia can hardly be seen. Upper Maastrichtian, Fresville (Cotentin, Manche). Presented by the author. × 20. D. 49845.

FIG. 3. Unilaminar fragment with large opesia. Some ovicells and an avicularium in the lower row of zooecia are visible. Upper Maastrichtian, Chef du Pont (Cotentin, Manche). × 20 Voigt Collection, Hamburg, Nr. 3909.

***Thyracella* cf. *meudonensis* (d'Orbigny) (p. 26)**

FIG. 4. Branched narrow fragment with an avicularium, for comparison with fig. 5. Upper Maastrichtian, Port Filiolet, (Cotentin, Manche). × 20. Voigt Collection, Hamburg, Nr. 3919.

FIG. 5. Damaged fragment of the bilaminar zoarium. From the matrix of D. 181. Upper Maastrichtian (Cotentin, Manche). × 20. D. 49588.

FIG. 6. Worn fragment, d'Orbigny Collection, Paris Nr. 8040, Musée d'Histoire Naturelle. labelled Meudon but likely Upper Maastrichtian, locality uncertain (? Néhou, Cotentin, Manche). × 20.

"*Membranipora unipora*" Marsson (p. 19)

FIG. 7. Fragment with hyperstomial ovicells and median pores on the gymnocyst of the undamaged zooecia. The minute marks of spines are hidden by recrystallization. From the rock matrix of D. 181. Upper Maastrichtian (Cotentin, Manche). × 20. D. 49576.

FIG. 8. Holotype, of *Flustrellaria simplex* d'Orbigny Collection, Nr. 8130, Musée d'Histoire Naturelle Paris, Upper Maastrichtian, Néhou (Cotentin, Manche). × 20.

***Bactrellaria rugica* Marsson (p. 24)**

FIG. 9. Small worn fragment showing the pits of the avicularia below the opesium. From the matrix of D. 181. Upper Maastrichtian (Cotentin, Manche). × 20. D. 49584.

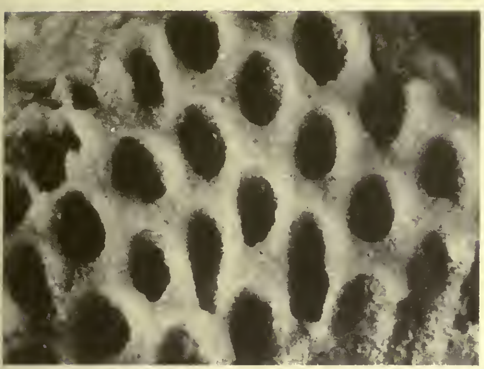
FIG. 10. The same specimen, showing the backside. × 20.

FIG. 11. Fragment with well preserved avicularia. Upper Maastrichtian, Port Filiolet (Cotentin, Manche). Presented by the author. × 20. D. 49585.

FIG. 12. Worn fragment in similar condition as figs. 9–10. Upper Maastrichtian, Port Filiolet (Cotentin, Manche). × 20. Voigt Collection, Hamburg, Nr. 3914.

FIG. 13. Well preserved fragment with raised avicularia whose rostra are damaged. From chalk of a flint-boulder of Upper Maastrichtian age, Wulmstorf near Harburg-Hamburg, Northern Germany. × 20. Voigt Collection, Hamburg, Nr. 4146.

FIG. 14. The same as fig. 13, lateral view, showing the long tubular peduncles of the avicularia. × 20.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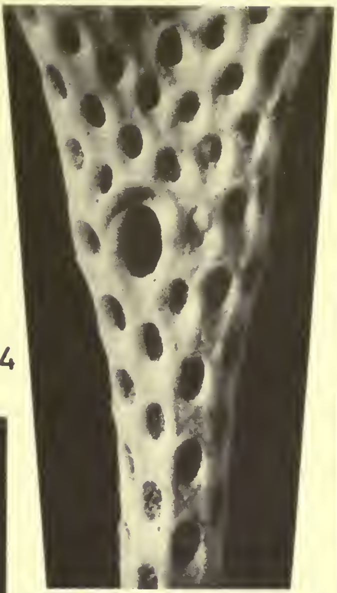
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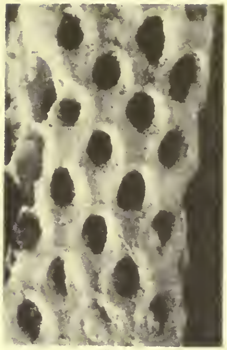
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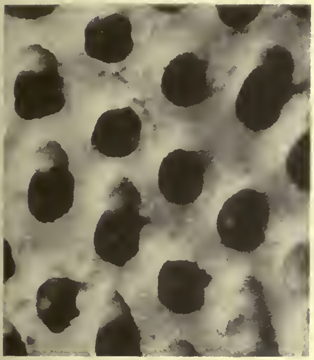
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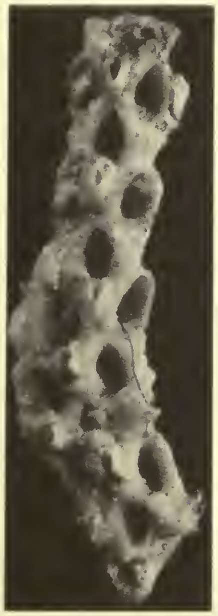
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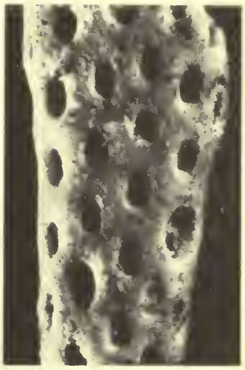
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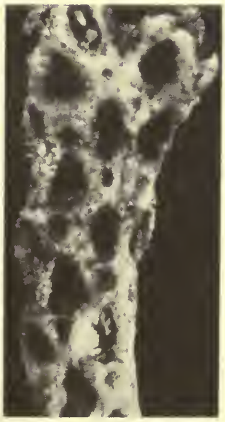
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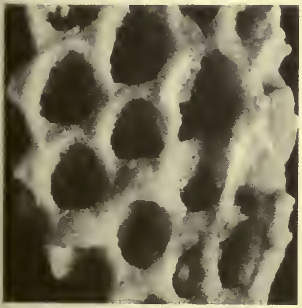
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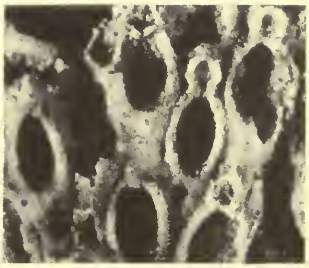
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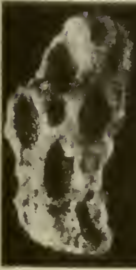
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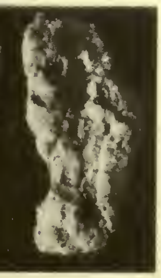
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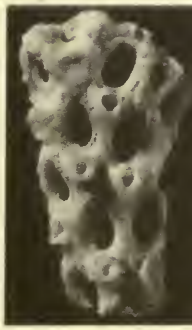
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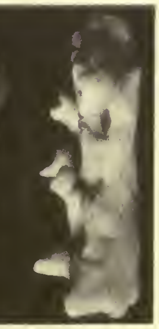
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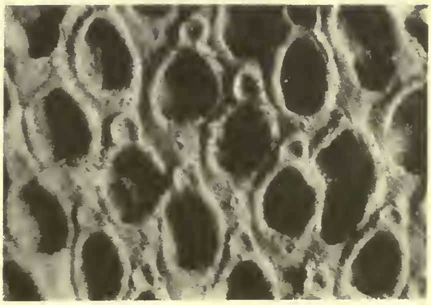
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PLATE 3

Stamenocella marginata d'Orbigny (p. 25)

Fig. 1. Fragment of the bilaminar zoarium in the matrix of *Onychocella piriformis* (Goldfuss) (D.181). Upper Maastrichtian (Cotentin, Manche). ×20. D.47322.

Fig. 2. Similar fragment. Upper Maastrichtian, Chef du Pont (Cotentin, Manche). Presented by the author. ×20. D.49586.

Fig. 3. Holotype of *Biflustra tesselata* d'Orbigny. Upper Maastrichtian, Néhou (Cotentin, Manche). d'Orbigny Collection, Nr. 8053, Paris Musée d'Histoire Naturelle. ×20.

Fig. 4. Holotype of *Biflustra marginata* d'Orbigny. Upper Maastrichtian, Sainte Colombe (Cotentin, Manche). d'Orbigny Collection, Nr. 8134, Paris Musée d'Histoire Naturelle. ×20.

Fig. 5. Well preserved large fragment showing the different aspect and size of zooecia and avicularia. The basal region represents *Flustrella convexa* d'Orbigny. Upper Maastrichtian, Chef du Pont (Cotentin, Manche). ×20. Voigt Collection, Hamburg, Nr. 4128.

Radulopora minor n. sp. (p. 22)

Fig. 6. Small worn bilaminar fragment from the matrix of D.181. Upper Maastrichtian, (Cotentin, Manche). ×20. D.49579.

Fig. 7. Fragment showing the gradual tapering of the zoarium. Upper Maastrichtian, Chef du Pont (Cotentin, Manche). Presented by the author. ×20. D.49580.

Fig. 8. Another fragment. Upper Maastrichtian, Chef du Pont (Cotentin, Manche). Presented by the author. ×20. D.49581.

Fig. 9. Broad fragment, most zooecia with ovicells on the right side with anen crusting Foraminifer. Upper Maastrichtian, Chef du Pont (Cotentin, Manche). Presented by the author. ×20. D.49582.

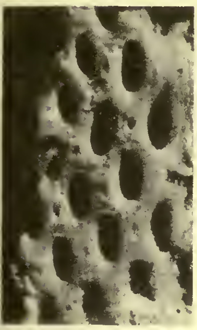
Fig. 10. Holotype, showing the larger marginal zooecia at the edge of the zoarium. Upper Maastrichtian, St. Pietersberg near Maastricht (Netherlands). ×20. Presented by the author. D.49844.

Radulopora radula (Marsson) (p. 21)

Fig. 11. Fragment of the thick bilaminar zoarium for comparison with *Radulopora minor* n. sp., showing the larger zooecia and avicularia and some fertile zooecia with broken ovicells. Upper Maastrichtian Chalk in drift, Tornesch near Elmshorn (Schleswig-Holstein, Northern Germany). ×20. Voigt Collection, Hamburg Nr. 3974.

Fig. 12. Singular vibraculum, ×120, showing the thornlike process which is curved inwards. Horizon, locality and collection as for fig. 11.

PLATE 3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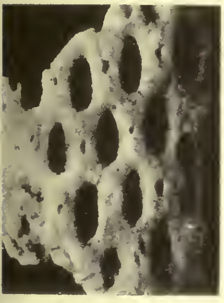
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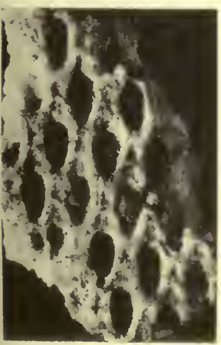
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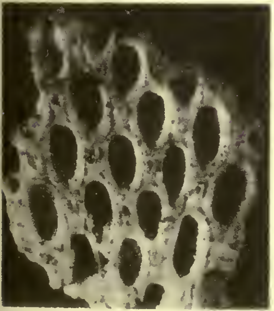
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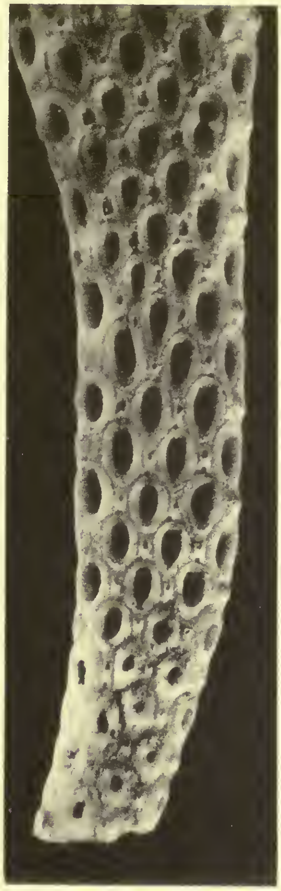
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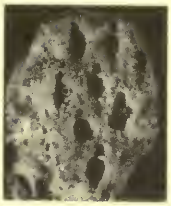
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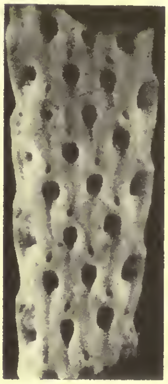
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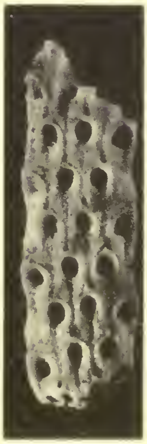
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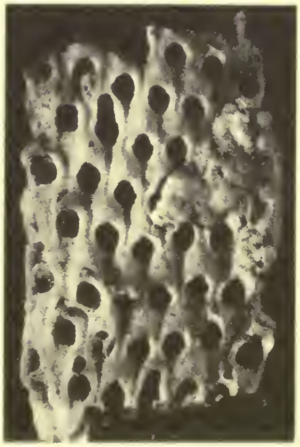
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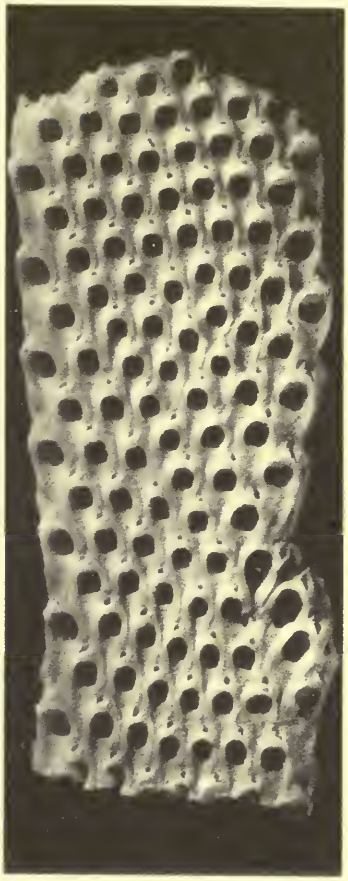
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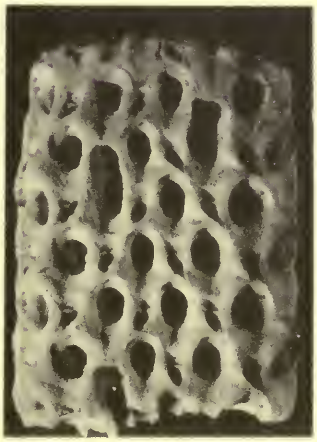
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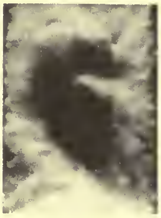
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PLATE 4

Amphiblestrella elegans (v. Hagenow) (p. 20)

FIG. 1. Small worn fragment from the matrix of D.181. Upper Maastrichtian (Cotentin, Manche). ×20. D.49577.

FIG. 2. Holotype of *Flustrella baculina* d'Orbigny. Upper Maastrichtian, Néhou (Cotentin, Manche). d'Orbigny Collection, Paris, Nr. 8127, Musée d'Histoire Naturelle. ×20.

FIG. 3. Branched fragment. Upper Maastrichtian, Chef du Pont (Cotentin, Manche). Presented by the author. ×20. D.49578.

Rosseliana thomasi n. sp. (p. 31) (see also pl. 1, fig. 6)

FIG. 4. Holotype, showing the encrusting zoarium upon a branched fragment of *Radulopora minor* n. sp. Upper Maastrichtian, Chef du Pont (Cotentin, Manche). Presented by the author. ×20. D.49597.

FIG. 5. Same specimen, part of the zoarium ×40, showing the form of the opesium and some fertile zooecia with ovicells.

FIG. 6. Zoarium encrusting an echinoid fragment. Upper Maastrichtian, Port Filiolet (Cotentin, Manche). ×20. Voigt Collection, Hamburg, Nr. 3932.

Floridina scutata (Levinsen) (p. 31)

FIG. 7. Part of encrusting zoarium, for comparison with *Rosseliana thomasi* n. sp. Upper Maastrichtian chalk boulder in drift, Tornesch near Elmshorn (Schleswig-Holstein, Northern-Germany). ×40. Voigt Collection, Hamburg, Nr. 4145.

Puncturiella cf. ***superba*** Brydone (p. 33)

FIG. 8. Small unilaminar fragment in matrix of D.181. Upper Maastrichtian (Cotentin, Manche). ×20. D.49598.

FIG. 9. Unilaminar fragment. Upper Maastrichtian, Chef du Pont (Cotentin, Manche). Presented by the author. ×20. D.49599.

FIG. 10. Unilaminar fragment, well preserved. Upper Maastrichtian, St. Pietersberg near Maastricht (Netherlands). Presented by the author. ×20. D.49600.

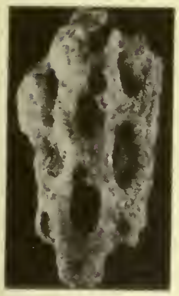
Semiescharinella complanata d'Orbigny (p. 29)

FIGS. 11–12. Small badly preserved unilaminar fragment from the matrix of D.181. Upper Maastrichtian (Cotentin, Manche). ×20. D.49595 and 49596.

FIG. 13. Fragment with well preserved zooecia and distal avicularia. Upper Maastrichtian, Chef du Pont (Cotentin, Manche). Presented by the author. ×20. D.49847.

FIG. 14. Small fragment showing one zooecium with ovicell in the right lower corner. Upper Maastrichtian, Chef du Pont (Cotentin, Manche). ×20. Voigt Collection, Hamburg, Nr. 3918b.

FIG. 15. Holotype of *Escharinella simplex* d'Orbigny. Upper Maastrichtian, Néhou (Cotentin, Manche). d'Orbigny Collection, Paris, Nr. 7942, Musée d'Histoire Naturelle. ×20.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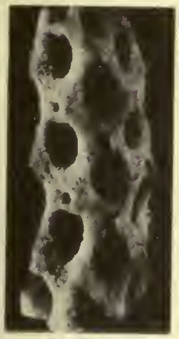
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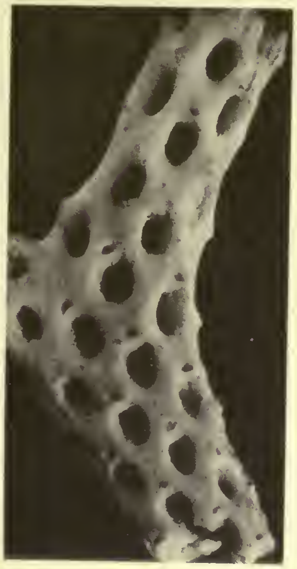
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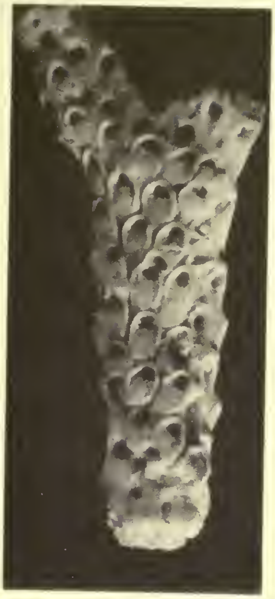
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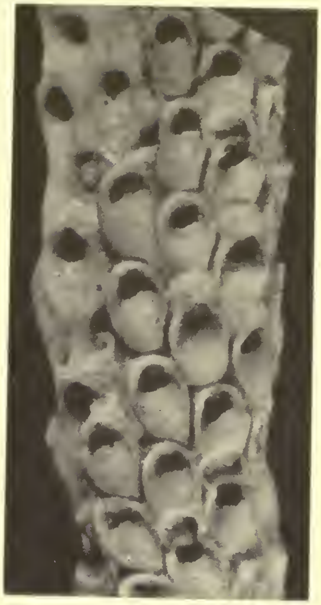
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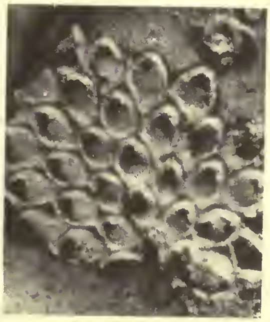
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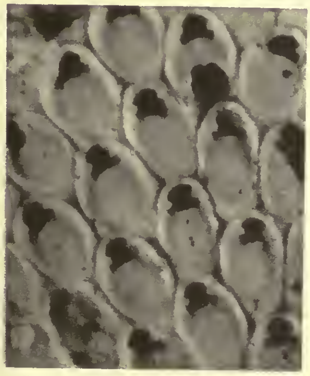
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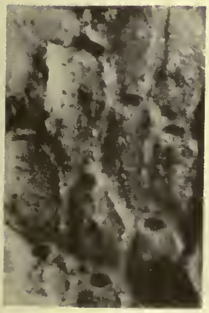
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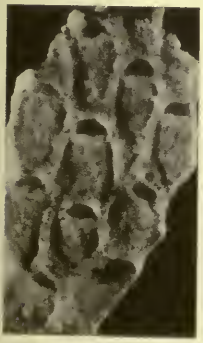
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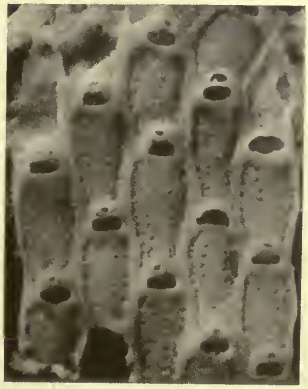
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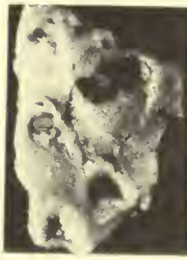
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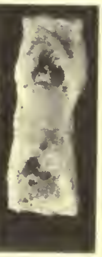
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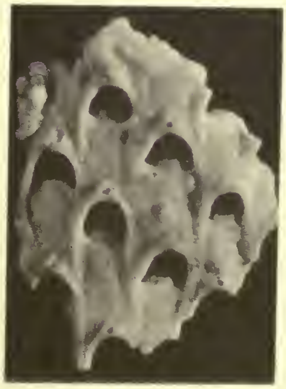
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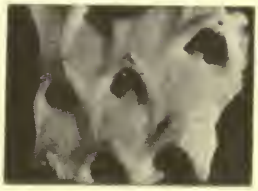
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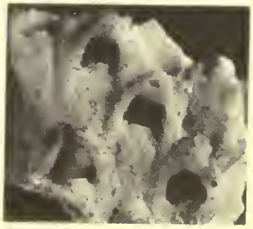
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PLATE 5

Onychocellaria caecilia (d'Orbigny) (p. 36)

FIG. 1. Fragment of a well preserved segment with some avicularia on the edges of the slightly flattened rods. Upper Maastrichtian, Chef du Pont (Cotentin, Manche). ×20. Presented by the author. D.49730.

FIG. 2. Same specimen seen from the narrow side with two avicularia. ×20.

FIG. 3. Another fragment with closed zooecia in the proximal region and larger opesia. Upper Maastrichtian, Chef du Pont (Cotentin, Manche). Presented by the author. ×20. D.49731.

FIG. 4. Small fragment with avicularium. From the matrix of D.181. Upper Maastrichtian, Chef du Pont (Cotentin, Manche). ×20. D.49726.

FIG. 5. Another fragment with avicularium in the middle row of zooecia. From the matrix of D.181. Upper Maastrichtian (Cotentin, Manche). ×20. Photographed under water. D.49727.

FIG. 6. Broad worn fragment. From the matrix of D.181. Upper Maastrichtian (Cotentin, Manche). ×20. Photographed under water. D.49767.

Vincularia canalifera (von Hagenow) (p. 27) (See also pl. 8, figs. 9–12.)

FIG. 7. Proximal part of a well preserved segment, showing more oval opesia and some zooecia with the characteristic openings for radicell filaments at the lower end. Upper Maastrichtian, Md., St. Pietersberg near Maastricht (Netherlands). ×20. Presented by the author. D.49840.

FIG. 8. Fragment with some avicularia in the distal and proximal part, showing more semicircular opesia than fig. 7. Upper Maastrichtian, Md., St. Pietersberg near Maastricht (Netherlands). ×20. Presented by the author. D.49841.

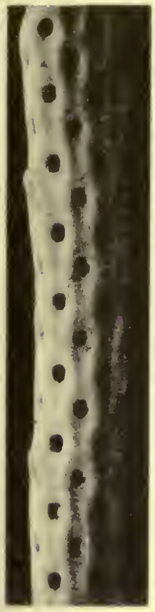
FIG. 9. Worn fragment. Upper Maastrichtian, Chef du Pont (Cotentin, Manche). ×20. Presented by the author. D.49734.

FIG. 10. Worn fragment. From the matrix of D.181. Upper Maastrichtian (Cotentin, Manche). ×20. D.49733.

Onychocella piriformis (Goldfuss) (p. 5)

FIG. 11. Fragment of the unilaminar frond with an avicularium in the lower left corner for comparison with fig. 12. Upper Maastrichtian, Chef du Pont (Cotentin, Manche). ×20. Voigt Collection, Hamburg, Nr. 3573.

FIG. 12. Holotype of *Onychocella bathonica* Gregory, erroneously labelled as "Bathonian Ranville (Calvados, France)", but certainly from the Upper Maastrichtian of the Cotentin (Manche). ×20. D.181.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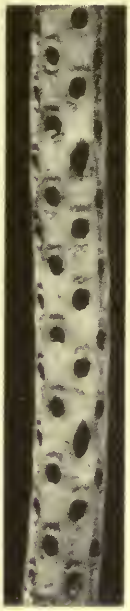
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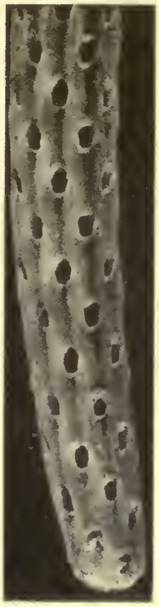
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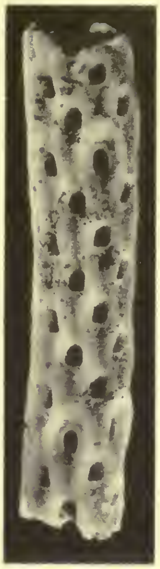
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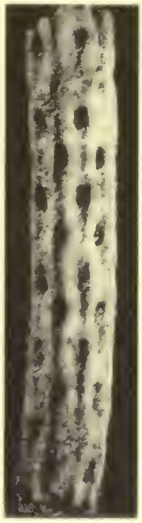
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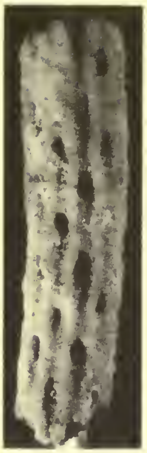
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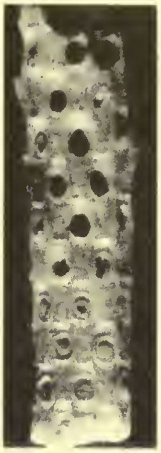
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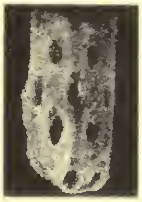
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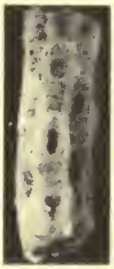
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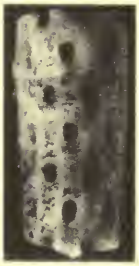
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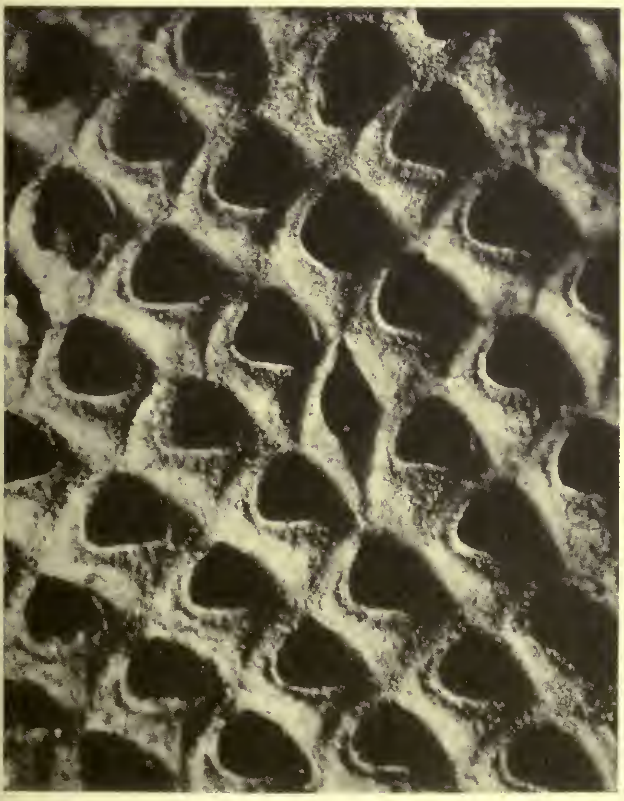
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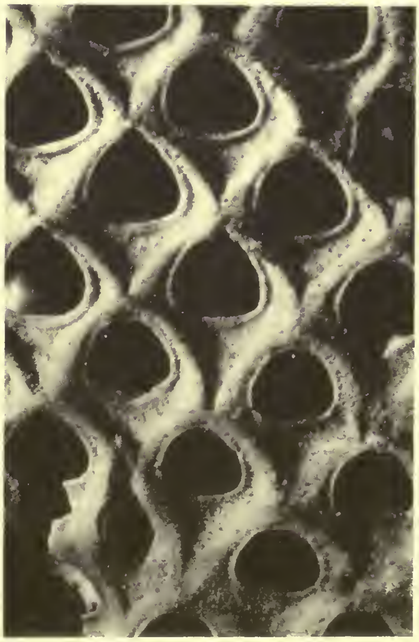
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PLATE 6

Onychocella cf. *cepha* d'Orbigny (p. 34)

Fig. 1. Branched fragment with some avicularia from the matrix of D.181. Upper Maastrichtian (Cotentin, Manche). ×20. D.49604.

Fig. 2. Fragment for comparison with fig. 1. Upper Maastrichtian, Chef du Pont (Cotentin, Manche). ×20. Presented by the author. D.49606.

Onychocella nysti (v. Hagenow) (p. 34)

Fig. 3. Worn fragment from the matrix of D.181. Upper Maastrichtian (Cotentin, Manche). ×20. D.49602.

Fig. 4. Well preserved specimen with two ovicells. Upper Maastrichtian, Chef du Pont (Cotentin, Manche). ×20. Presented by the author. D.49603.

Onychocella bellona (d'Orbigny) (p. 35)

Fig. 5. Well preserved fragment with several ovicells. Upper Maastrichtian, Néhou (Cotentin, Manche). ×20. d'Orbigny Collection, Paris, Nr. 7812.

Fig. 6. Fragment from the Upper Maastrichtian from Chef du Pont (Cotentin, Manche) intermediate between fig. 5 and fig. 7. Presented by the author. ×20. D.49608.

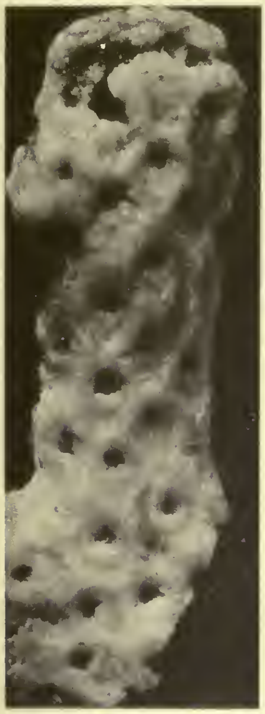
Fig. 7. Worn fragment from the matrix of D.181. Upper Maastrichtian (Cotentin, Manche). ×40. D.49607.

Quadricellaria elegans d'Orbigny (p. 29)

Fig. 8. Fragment of a segment. Upper Maastrichtian (Cotentin, Manche). From the matrix of D.181. ×20. D.49591.

Fig. 9. Another worn fragment. Upper Maastrichtian (Cotentin, Manche). From the matrix of D.181. ×20. D.49592.

Fig. 10. Fragment with a large avicularium. Upper Maastrichtian, Chef du Pont (Cotentin, Manche). ×40. Voigt Collection, Hamburg, Nr. 4133.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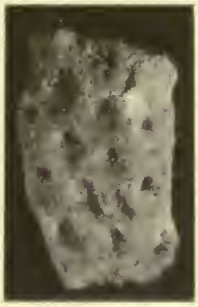
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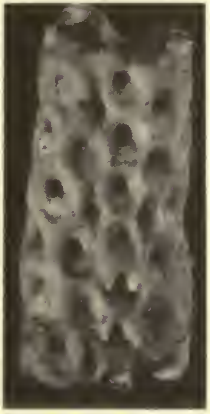
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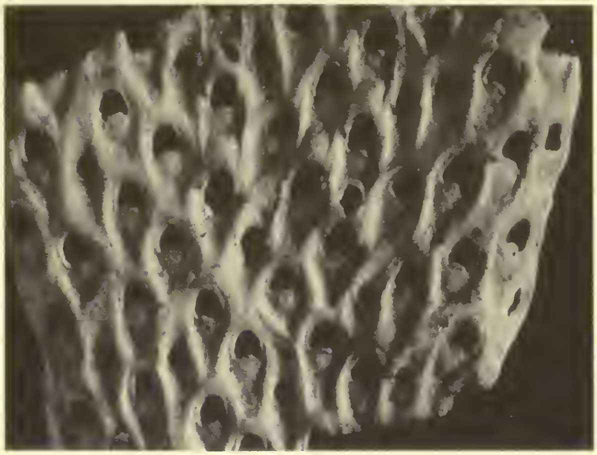
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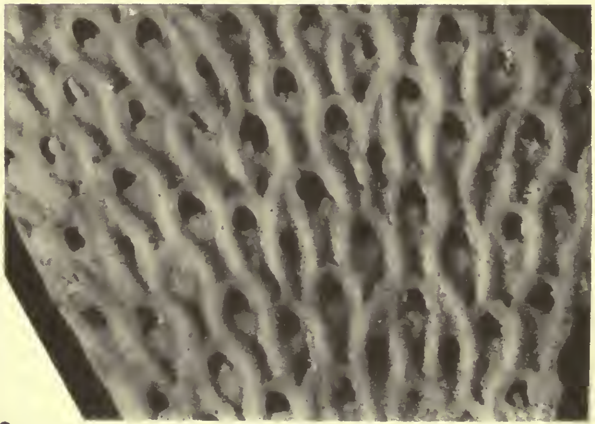
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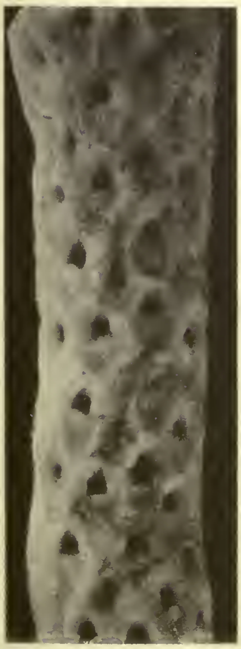
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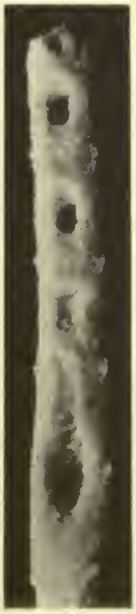
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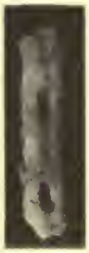
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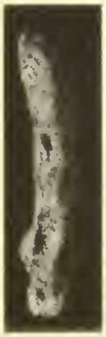
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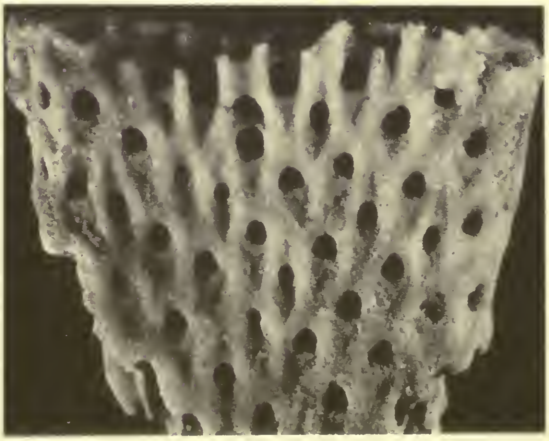
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PLATE 7

Decurtaria cf. ***cornuta*** (Beissel) (p. 37)

FIG. 1. Zoarium with ancestrula and one ovicelled zooecium. From the matrix of D.181. Upper Maastrichtian (Cotentin, Manche). ×20. D.49609.

FIG. 2. Incomplete zoarium with some ovicelled zooecia. Upper Maastrichtian, Chef du Pont (Cotentin, Manche). ×20. Voigt Collection, Hamburg, Nr. 4137.

Pliophloea sp. (p. 37)

FIG. 3. Young zoarium with ancestrula and one ovicelled zooecium. In the matrix of *Castanopora jurassica* (Gregory) D.180. Upper Maastrichtian (Cotentin, Manche). ×20. D.47324.

Castanopora jurassica (Gregory) (p. 7)

FIG. 4. Bilaminar fragment with two ovicelled zooecia. Upper Maastrichtian, Chef du Pont (Cotentin, Manche). Presented by the author. ×20. D.49724.

FIG. 5. Same specimen from the other side, showing one zooecium with preserved frontal wall. ×20.

FIG. 6. Fragment with some zooecia. Upper Maastrichtian, Chef du Pont (Cotentin, Manche). ×20. Voigt Collection, Hamburg, Nr. 3585.

FIG. 7. Part of a young zoarium with smaller zooecia. Upper Maastrichtian, Chef du Pont (Cotentin, Manche). Presented by the author. ×20. D.49725.

" ***Membranipora*** " ***constricta*** d'Orbigny (p. 13)

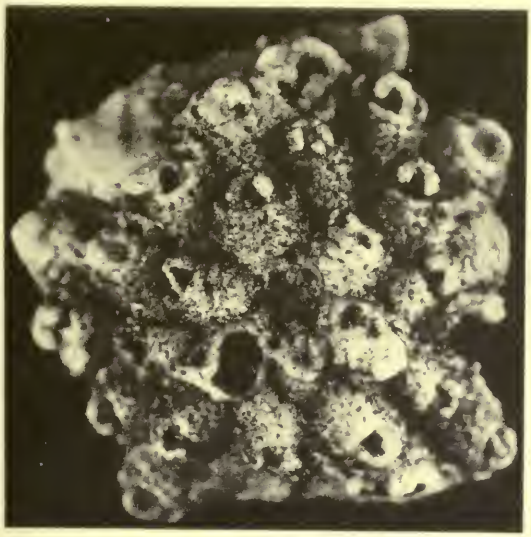
FIG. 8. Badly preserved specimen encrusting a Brachiopod. Aptian les Croutes (Yonne, France) ? Holotype, d'Orbigny Collection, Paris, Musée d'Histoire Naturelle, Nr. 5691. ×20.

Micropora transversa (d'Orbigny) (p. 32)

FIG. 9. Small worn fragment showing the two opesiular pores below the opesium. From the matrix of D.181. Upper Maastrichtian (Cotentin, Manche). ×20. D.49768.

FIGS. 10–11. Two fragments of the Holotype. Upper Maastrichtian, Néhou (Cotentin, Manche). ×20. d'Orbigny Collection, Paris, Musée d'Histoire Naturelle, Nr. 7755.

FIG. 12. Fragment, Upper Maastrichtian, Chef du Pont (Cotentin, Manche). ×20. Presented by the author. D.49769.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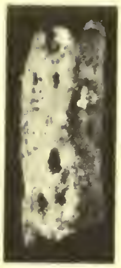
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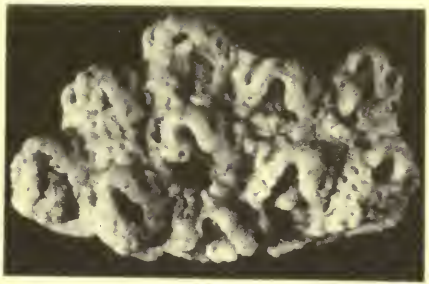
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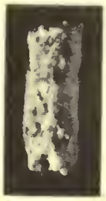
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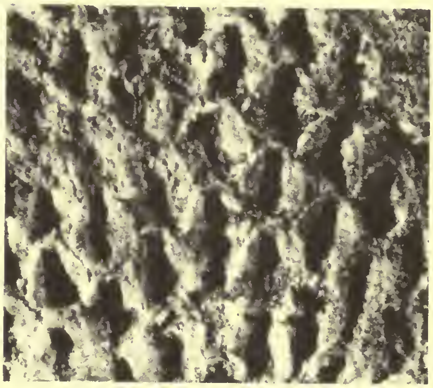
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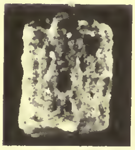
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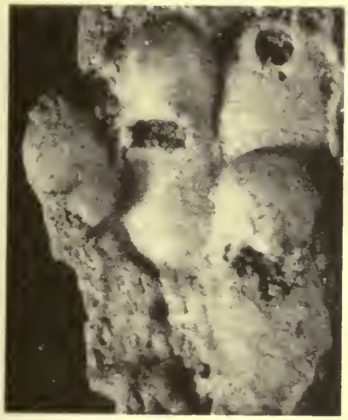
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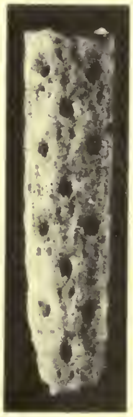
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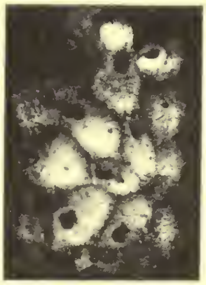
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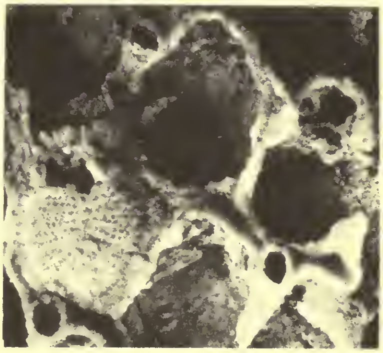
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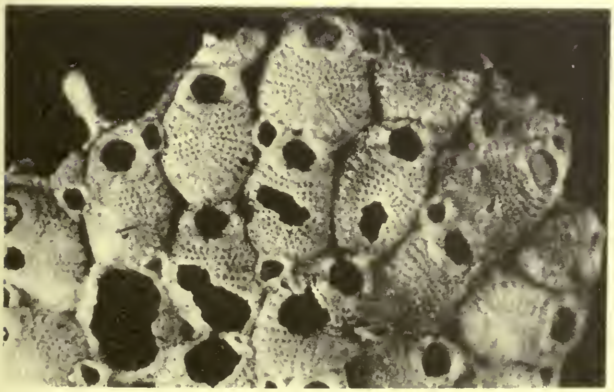
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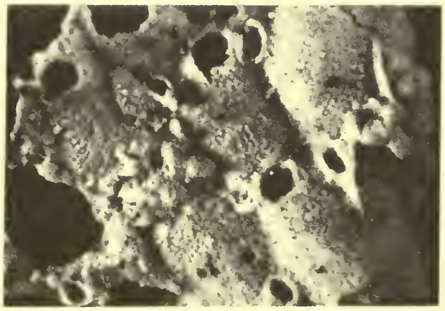
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PLATE 8

Beisselinopsis flabellata (d'Orbigny) (p. 40)

FIG. 1. Adult zoarium. Upper Maastrichtian, Chef du Pont (Cotentin, Manche). ×20. Voigt Collection, Hamburg, Nr. 3908.

FIG. 2. Young worn zoarium. From the matrix of D.181. Upper Maastrichtian (Cotentin, Manche). ×20. D.49723.

Beisselina striata (Goldfuss) (p. 39)

FIG. 3. Worn fragment. From the matrix of D.181. Upper Maastrichtian (Cotentin, Manche). ×20. D.49721.

FIG. 4. Worn fragment for comparison with fig. 3. Upper Maastrichtian, Md., Geulem near Berg, Geul-valley near Maastricht (Netherlands). Presented by the author. ×20. D.49722.

Frurionella fertilis n. sp. (p. 38)

FIG. 5. Holotype, well preserved fragment with ovicelled zooecia. Upper Maastrichtian, Chef du Pont (Cotentin, Manche). Presented by the author. ×20. D.49610.

FIG. 6. Fragment showing zooecia with damaged ovicells. Upper Maastrichtian, Chef du Pont (Cotentin, Manche). Presented by the author. ×20. D.49612.

FIG. 7. Worn fragment, similar to fig. 6. From the matrix of D.181. Upper Maastrichtian (Cotentin, Manche). ×20. D.49611.

Frurionella europaea (Voigt) (p. 39)

FIG. 8. For comparison with *Frurionella fertilis* n. sp. Upper Maastrichtian, Chef du Pont (Cotentin, Manche). Presented by the author. ×20. D.49720.

Vincularia canalifera (v. Hagenow) (p. 27) (See also pl. 5, figs. 7–10)

FIG. 9. Small fragment. From the matrix of D.181. Upper Maastrichtian (Cotentin, Manche). ×20. D.49735.

FIG. 10. Badly preserved branched fragment showing an avicularium in the middle of the right side. From the matrix of D.181. Upper Maastrichtian (Cotentin, Manche). ×20. D.49736.

FIG. 11. Fragment showing an avicularium at the right upper corner. Upper Maastrichtian Md., Geulem near Berg, Geul-valley near Maastricht (Netherlands). ×20. D.49842. E. Voigt Collection.

FIG. 12. Part of a branched stem, for comparison with fig. 9, showing relatively small zooecia and opesia. Upper Maastrichtian, locality as fig. 11. D.49732.

Vincularia concinna (d'Orbigny) (p. 28)

FIG. 13. Holotype. Branched fragment for comparison with *Vincularia canalifera* von Hagenow. Upper Maastrichtian, Néhou (Cotentin, Manche). ×20. d'Orbigny Collection, Paris, Musée d'Histoire Naturelle, Nr. 7756.

Vincularia flexuosa (d'Orbigny) (p. 28)

FIG. 14. Holotype. Fragment for comparison with *Vincularia canalifera* von Hagenow. Labelled as Santonian Vendôme, Loir et Cher, France. ×20. d'Orbigny Collection, Paris, Musée d'Histoire Naturelle, Nr. 7752.

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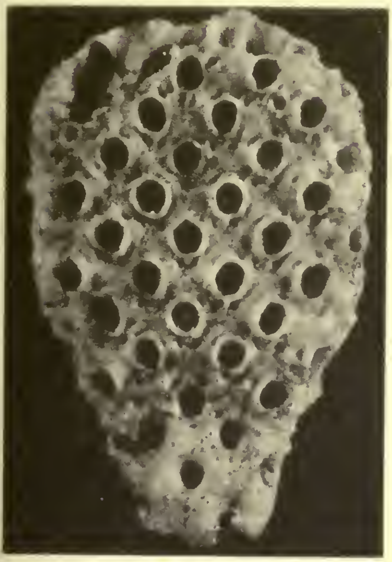
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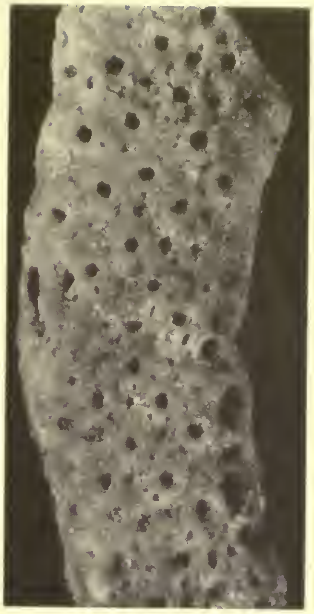
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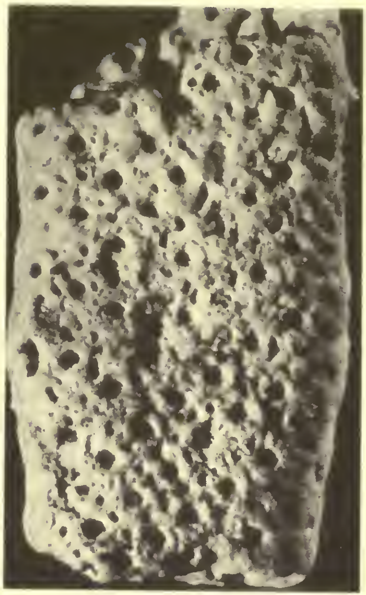
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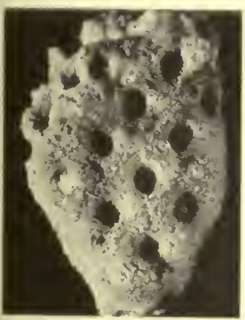
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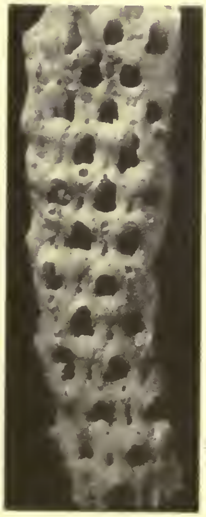
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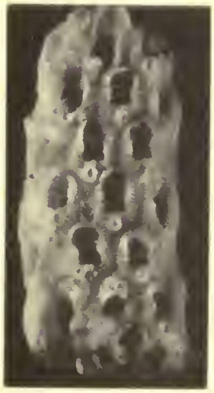
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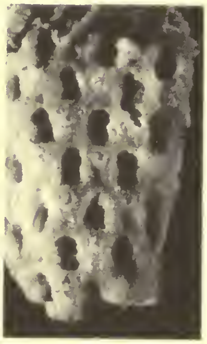
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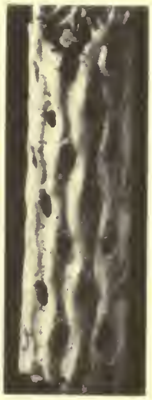
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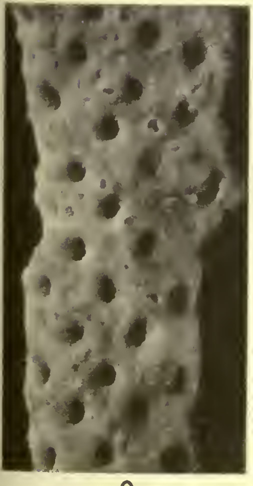
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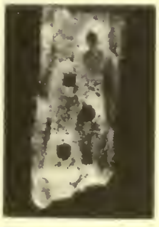
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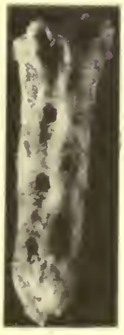
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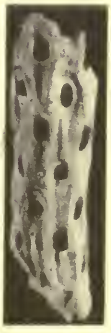
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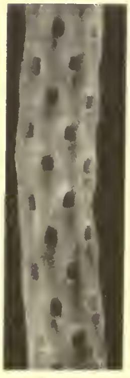
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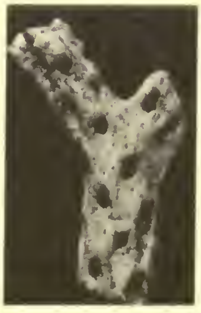
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THE CAUDAL SKELETON IN MESOZOIC ACANTHOPTERYGIAN FISHES

COLIN PATTERSON

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
GEOLOGY Vol. 17 No. 2
LONDON: 1968

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BY

COLIN PATTERSON
British Museum (Natural History)

Pp. 47–102; 28 *Text-figures*

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By COLIN PATTERSON

CONTENTS

Page
I. INTRODUCTION 49
II. SYSTEMATIC DESCRIPTIONS 50
  Order Ctenothrissiformes 50
  Order Beryciformes 56
    Suborder Polymixioidei 56
    Suborder Dinopterygoidei 62
    Suborder Berycoidei 67
  Order Lampridiformes 78
  Order Salmoniformes, Suborder Myctophoidei . . . 81
III. DISCUSSION 83
  (a) The relationships of Ctenothrissiformes, Myctophoidei and Beryciformes 83
  (b) The origin of Perciformes 87
  (c) Intermediate groups 96
IV. CONCLUSIONS 98
V. REFERENCES 100
VI. ABBREVIATIONS USED IN FIGURES 102

SYNOPSIS

This paper contains descriptions of the caudal skeleton in all Ctenothrissiformes and Mesozoic acanthopterygians, comparisons with living relatives being made where possible, and a brief account of the caudal skeleton in Mesozoic Myctophoidei. These groups have a basically similar caudal skeleton with the first ural and pre-ural centra fused, the second ural centrum free, six hypurals, three epurals, a stegural and a second uroneural. Caudal scutes persist in Ctenothrissiformes and primitive Myctophoidei and there is a single urodermal in some Cretaceous myctophoids.

The bearing of caudal structure on the origin and early evolution of acanthopterygians is discussed and variations in the second pre-ural neural spine are shown to be important. This structure is primitively short and slender: two opposite developments from this condition are elongation of the spine to support procurrent fin-rays (as in Polymixioidei) and reduction to a low crest (as in Berycoidei and Perciformes). Wherever a full second pre-ural neural spine occurs in perciform and higher groups it is produced secondarily by fusion with the first epural. The evidence of the caudal skeleton does not support a polyphyletic origin of Perciformes from different groups of Beryciformes. The Berycoidei appear to be the beryciform group most closely related to the Perciformes.

The Danian *Bathysoma* is shown to be a lampridiform: the lampridiforms probably arose from near *Aipichthys* and *Pharmacichthys*. The Zeiformes are close relatives of the Berycoidei.

I. INTRODUCTION

IN an earlier paper (Patterson 1964) I gave detailed accounts of the skeletal anatomy of the known Mesozoic acanthopterygian fishes (see also Patterson 1967) but without describing the caudal skeleton. This was omitted because when the bulk of the work was done there existed no comprehensive description or even terminology of the caudal skeleton of living teleosts. But during the last few years, following from the work of Gosline (1960), the caudal skeleton has become recognized as an important structure in tracing the relationships of teleost fishes and we now have both a satisfactory terminology (Gosline 1960; Nybelin 1963; Monod 1967; Patterson 1968) and a reasonable idea of the composition of the caudal skeleton in most teleostean groups (Gosline 1960, 1961, 1961*a*, 1963, 1965; Norden 1961; Rosen 1962, 1964; Greenwood, Rosen, Weitzman & Myers 1966; Monod 1967; Greenwood 1967; Weitzman 1967). In the light of this new information it seemed that an investigation of the caudal skeleton in Mesozoic acanthopterygians might prove a useful check on hypotheses of the origins of acanthopterygians and paracanthopterygians (Greenwood *et al.* 1966). Also included are accounts of caudal structure in the Ctenothrissiformes and, more briefly, in the Mesozoic Myctophoidei.

The terminology used here is that of Nybelin (1963) with the distinction between " urodermal " and " uroneural " introduced by Patterson (1968) and the addition from Monod (1967) of the terms " parhypural ", for the haemal arch of the first pre-ural centrum, the terminal structure perforated by the caudal vein and artery and which bears the hypurapophysis (Nursall 1963), and " stegural " for the paired structure which articulates with the dorso-lateral surface of the first pre-ural centrum and has a slender shaft extending postero-dorsally, lateral to the nerve cord. Monod considers the stegural to be an element *sui generis*, not a compound structure. In my opinion (Patterson 1968), the stegural represents the first uroneural fused with neural arch material from the first pre-ural and first ural vertebrae. The term stegural is nevertheless useful, since it obviates repetition of the cumbersome term " first uroneural fused with the neural arches of the first ural and pre-ural centra ".

The material used is mainly in the collections of the British Museum (Natural History): these specimens are referred to by a registered number without prefix or with the prefix " P ". Specimens from the American University, Beirut, the American Museum of Natural History, New York, the Royal Scottish Museum, Edinburgh, and the United States National Museum, Washington, are referred to with the prefixes " AUB ", " AMNH ", " RSM " and " USNM " respectively. The illustrations of fossil species are not reconstructions but *camera lucida* drawings of single specimens.

I am grateful to Drs. P. H. Greenwood and D. E. Rosen, who have read and criticized parts of this paper in manuscript, and for the loan of specimens to Prof. T. Raven, American University, Beirut, Drs. C. D. Waterston and R. S. Miles, Royal Scottish Museum, Dr. Bobb Schaeffer, American Museum of Natural History, and Drs. D. H. Dunkle and D. M. Cohen, United States National Museum.

II. SYSTEMATIC DESCRIPTIONS

Order CTENOTHRISSIFORMES (Patterson 1964 : 218)

According to Marshall (1961) the living *Macristium chavesi* is a surviving ctenothrissiform (see also Greenwood, Rosen, Weitzman & Myers 1966; Patterson 1967 : 86). Unfortunately, the only extant specimen of *Macristium* is a post-larval individual and the caudal skeleton is not ossified. But there appear to be six hypurals, as in Ctenothrissiformes. Berry & Robins (1967) have described a second macristiid, *Macristiella perlucens*, known only by a single post-larval specimen. In this fish there are six hypurals, as in Ctenothrissiformes, but Berry & Robins think it unlikely that the Macristiidae are close to the Ctenothrissiformes.

Family **AULOLEPIDIDAE** Patterson (1964 : 247)

Genus ***PATEROPERCA*** Smith Woodward (1942 : 543)

The type and only species, *P. libanica* Smith Woodward from the Middle Cenomanian of Hajula, Lebanon, is known only by two specimens, AUB 108906 (the holotype) and AUB 108904. In 108904 the caudal region is badly preserved and yields no useful information, but in the holotype the caudal skeleton is very well preserved (Fig. 1). The second pre-ural centrum (*pu2*) has a fully developed neural spine (*npu2*) and an autogenous haemal arch. It is not possible to see with certainty whether the haemal arch of the third pre-ural centrum (*pu3*) is autogenous. The first pre-ural and first ural centra are fused (*pu1* + *u1*), these fused centra bearing the parhypural (*ph*) and the first and second hypurals (*h1*, *h2*) in the normal way. The first hypural is rather slender, only a little broader than the parhypural and

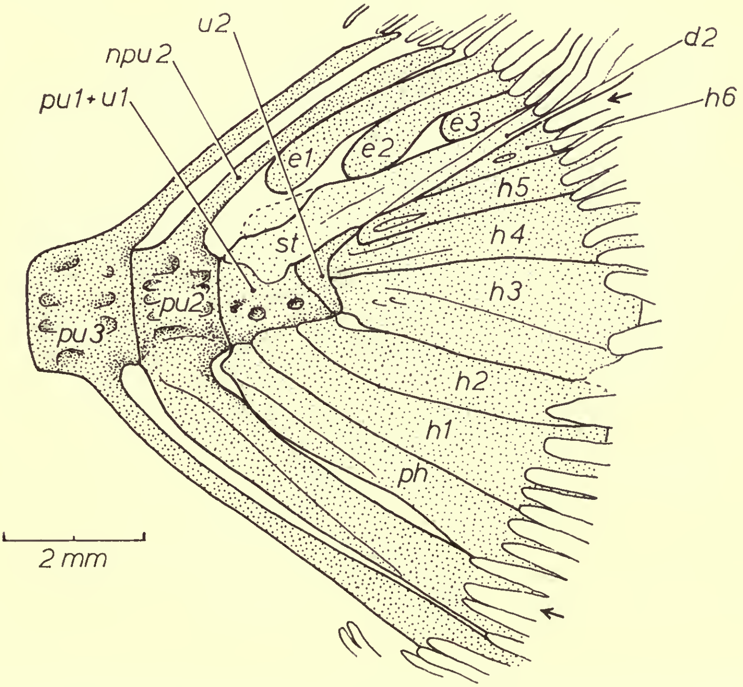


FIG. 1. *Pateroperca libanica* Smith Woodward. Caudal skeleton of the holotype, AUB 108906, standard length 86 mm., Middle Cenomanian, Hajula, Lebanon. For explanation of lettering see p. 102. Arrows mark the outermost (unbranched) principal fin-rays.

the second. Dorsally, the fused first pre-ural and ural centra bear a large stegural (*st*) and there is a second uroneural (*d2*) ending, as usual, in front of the base of the first unbranched principal ray of the caudal fin. There are three epurals (*e1 — 3*), the third small and short. There is a small independent second ural centrum (*u2*) bearing three hypurals (*h3 — 5*) decreasing in size upwards, and above these there is a small sixth hypural (*h6*) which probably failed to make contact with the ural centrum. The foremost procurrent rays of the caudal fin, which are unsegmented lepidotrichia, not spines, are inserted in front of the neural and haemal spine of the third pre-ural centrum. The uppermost principal ray of the fin (unbranched) is preceded by nine rays, only the last two or three segmented, and the lowermost by seven rays, the last two segmented.

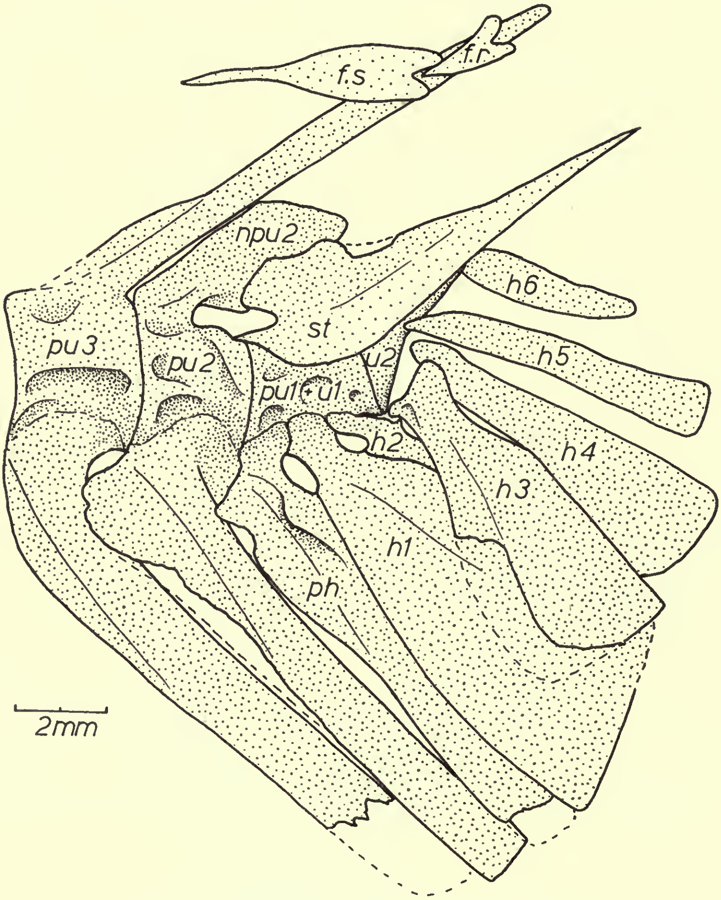


Fig. 2. *Aulolepis typus* Agassiz. Caudal skeleton of 47932, standard length *c.* 165 mm., Lower Chalk, Burham, Kent. *f. r*, foremost procurrent fin-ray (displaced); for explanation of other lettering see p. 102. The upper hypurals are displaced ventrally, the epurals and second uroneural are missing.

Genus ***AULOLEPIS*** Agassiz (1844 : 109)

In the type and only species, *A. typus* Agassiz from the Upper Cenomanian of the English Chalk, only two specimens show any details of the caudal skeleton, 4033 (the holotype, Fig. 3) and 47932 (Fig. 2), and in both the bones are disturbed to some extent. The caudal skeleton of *Aulolepis* agrees with that of *Pateroperca* in most respects: fusion of the first pre-ural and first ural centra (*pu1* + *u1*), presence of a free second ural centrum (*u2*), three epurals (*e1* — *3*), six hypurals (*h1* — *6*) of which the first and the third are largest, an autogenous haemal arch on the second pre-ural centrum (*pu2*), a stegural (*st*) and a free second uroneural (*d2*). The haemal arch of the third pre-ural centrum (*pu3*) appears to be autogenous in 47932 but fused with the centrum in 4033. *Aulolepis* differs clearly from *Pateroperca* in having the neural spine of the second pre-ural centrum developed as a low, broad crest (*npu2*) whose hind edge fits between the front edges of the stegurals. In my earlier descriptions of *Aulolepis* and *Pateroperca* (Patterson 1964 : 247) I discussed the difficulty of separating the two genera and considered the possibility that *P. libanica* is merely

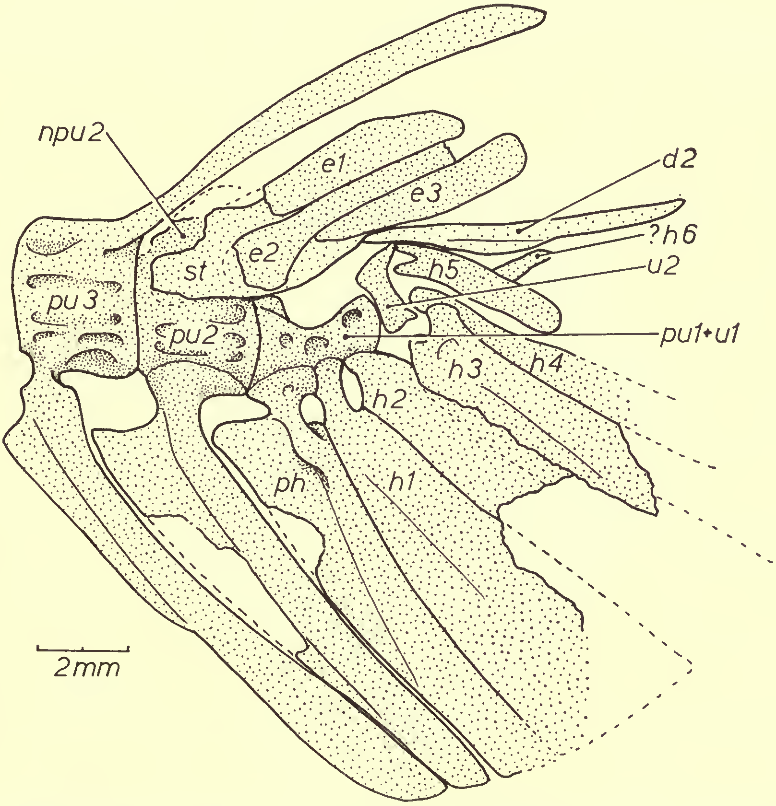


Fig. 3. *Aulolepis typus* Agassiz. Caudal skeleton of the holotype, 4033, standard length *c.* 135 mm., Lower Chalk, Lewes, Sussex. For explanation of lettering see p. 102. The epurals and upper hypurals are displaced ventrally, the stegural is displaced forwards.

a species of *Aulolepis*, but the presence on the second pre-ural centrum of a fully developed neural spine in *Pateroperca* and of a low crest in *Aulolepis* clearly separates the two genera. The caudal of 47932 shows one other point of interest, a slender, elongated caudal scute (*f. s*, Fig. 2) in front of the upper lobe of the fin. There is no conclusive evidence of a similar structure in front of the lower lobe of the fin, but it was probably present since there is a caudal scute in front of each lobe of the fin in *Ctenothrissa* (see below) and in most living teleosts which still retain these structures (*Elops*, *Tarpon*, *Albula*, *Aulopus* and *Chanos*, Gosline 1965 : 192; *Argentina*, Weitzman 1967 : 532). There is no sign of caudal scutes in either specimen of *Pateroperca*, but again it is probable that they were present. No specimen of *Aulolepis* has the fin-rays of the caudal fin well preserved but 4033 shows that the foremost procurrent rays of the lower lobe articulated with the haemal spine of the third pre-ural centrum, and both 4033 and 47932 show that these foremost rays were true spines.

Family **CTENOTHRISSIDAE** Smith Woodward (1901)

Genus ***CTENOTHRISSA*** Smith Woodward (1899 : 490)

In *Ctenothrissa*, the only genus of the Ctenothrissidae, the caudal skeleton and fin are well exposed in the two species from the Cenomanian of the Lebanon, *C. vexillifer*

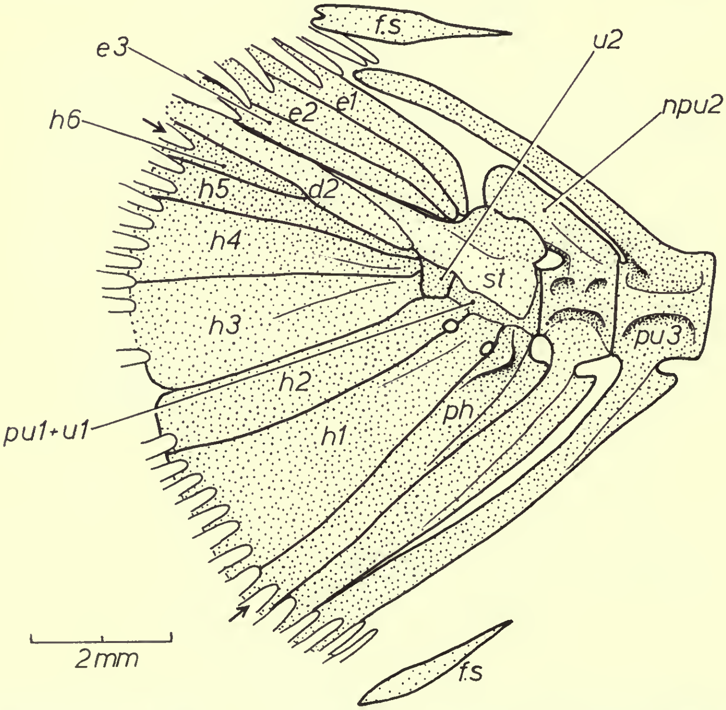


FIG. 4. *Ctenothrissa signifer* Hay. Caudal skeleton of P. 47524, standard length 83 mm., Middle Cenomanian, Hajula, Lebanon. For explanation of lettering see p. 102. Arrows mark the outermost (unbranched) principal fin-rays.

(Pictet 1850), the type species, and *C. signifer* Hay (1903) (Fig. 4), and the caudal skeleton is preserved in one or two specimens of *C. microcephala* (Agassiz) (Fig. 5) and *C. radians* (Agassiz) from the Upper Cenomanian of the English Chalk. There seem to be no significant differences in caudal anatomy between these four species. As in Aulolepididae, there is a free second ural centrum (*u2*), the first ural and first pre-ural centra are fused (*pu1* + *u1*), there are six hypurals (*h1* — 6), the first and third the largest and the sixth failing to articulate with the second ural centrum, there are three epurals (*e1* — *3*), a stegural (*st*) and a second uroneural (*d2*) and the haemal arch of the second pre-ural centrum (*pu2*) is autogenous. The haemal arch of the third pre-ural centrum (*pu3*) appears partially or completely fused to the centrum. As in *Aulolepis*, but in contrast to *Pateroperca*, the neural spine of the second pre-ural centrum (*npu2*) is represented by a broad crest, about half as high as the preceding spine. There is a slender caudal scute (*f. s.*) in front of both the upper and lower lobes of the caudal fin. In *C. vexillifer* and *C. signifer*, the only species in which the caudal fin-rays are well preserved, both the upper and lower principal rays are preceded by six rays, the last two segmented, and the foremost fin-rays are inserted on the neural and haemal spines of the third pre-ural centrum.

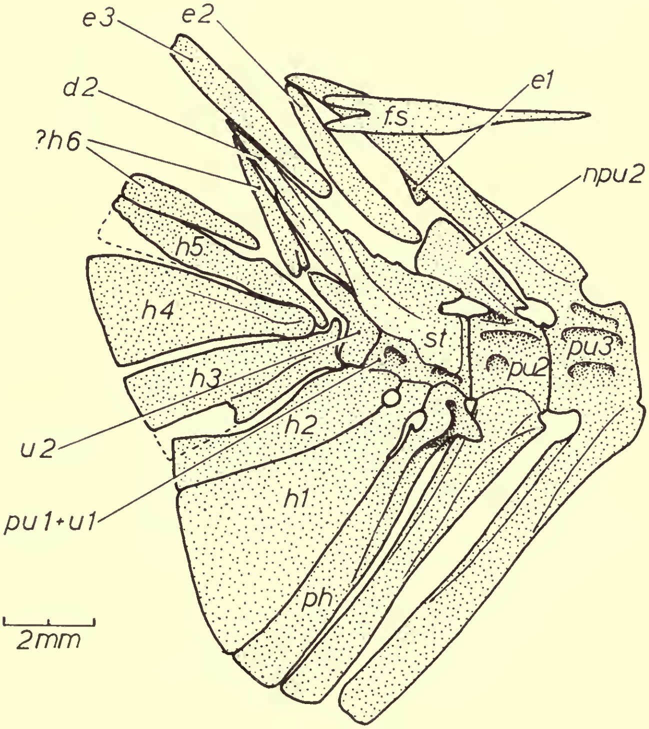


FIG. 5. *Ctenothrissa microcephala* (Agassiz). Caudal skeleton of 49881, standard length *c.* 115 mm., Lower Chalk, zone of *Holaster subglobosus*, Reigate, Surrey. For explanation of lettering see p. 102. The upper hypurals are displaced ventrally. Of the two elements labelled *? h6*, that on the left may be the base of a fin-ray.

In these small species from the Lebanon, the foremost procurrent caudal rays are unsegmented lepidotrichia, with separate right and left halves, but in the larger species from the English Chalk they appear to be true spines.

Order BERYCIFORMES

Suborder POLYMIXIOIDEI Patterson (1964 : 433)

Family **POLYMIXIIDAE** Gill (1862)

The only living genus of this family and suborder is *Polymixia*. The caudal skeleton of *Polymixia nobilis* has been figured by Regan (1911, fig. 1) and briefly discussed by Gosline (1961 : 14). The specimen illustrated here (Fig. 6) is almost certainly that used by Regan. The haemal arches of the second and third pre-ural centra (*pu2*, *pu3*) are autogenous, the second pre-ural centrum has a fully developed neural spine (*npu2*), the first pre-ural and first ural centra are fused (*pu1* + *u1*) and there is a free second ural centrum (*u2*). There is a large stegural (*st*) and a free second uroneural (*d2*). There are three slender epurals (*e1* — *3*) and six hypurals (*h1* — *6*) of which the first and the fourth are the largest, the third being excavated posteroventrally to give a notch between the hypurals supporting the upper and lower lobes of the fin. The second ural centrum has a long posterior process and makes contact with the sixth hypural. The first rays of the caudal fin articulate with the neural and haemal spines of the third pre-ural centrum. In the upper lobe of the fin the first unbranched principal ray is preceded by four true spines and two

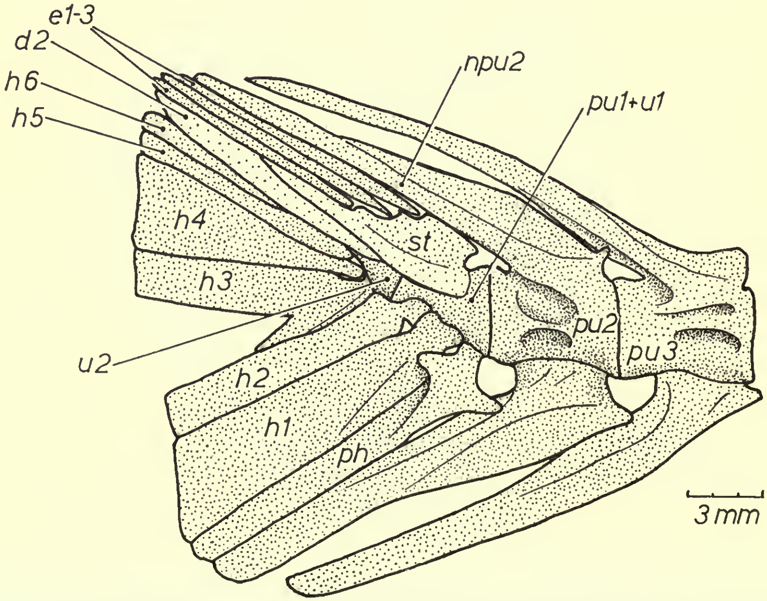


FIG. 6. *Polymixia nobilis* Lowe. Caudal skeleton of a dried skeleton, 1895.5.28.1, standard length 220 mm., Madeira. For explanation of lettering see p. 102.

segmented rays, in the lower lobe by three spines and two segmented rays. A caudal skeleton of *P. japonicus* does not differ from that of *P. nobilis*.

Genus ***BERYCOPSIS*** Dixon (1850 : 372)

In the type species, *B. elegans* Dixon from the Upper Cenomanian and Turonian of the English Chalk, the caudal skeleton is well preserved in 25881 (Fig. 7) and P.6465. The caudal skeleton of *B. elegans* agrees with that of *Polymixia* in almost every detail except that the third hypural (*h3*) is not excavated postero-ventrally so that it is as large as the fourth, the haemal arch of the third pre-ural centrum, probably autogenous in P.6465, is fused with the centrum in 25881, and the third and fourth hypurals, separate in 25881 (standard length *c.* 13 cm.), are completely fused in the larger P.6465 (standard length *c.* 16 cm.). In 25881 the lateral surface of the second ural centrum is covered by a small, triangular plate (*x*, Fig. 7). P.6465 is not sufficiently well preserved to see whether this plate is present. The plate appears to be part of the caudal skeleton, not a dermal element which has become apposed to the centrum *post mortem*. The only record of a similar structure is in the living myctophoid *Synodus foetens*, where Hollister (1937*a*, figs. 5, 12) found a " uroneural " in this position, ventral to the normal uroneurals. The foremost

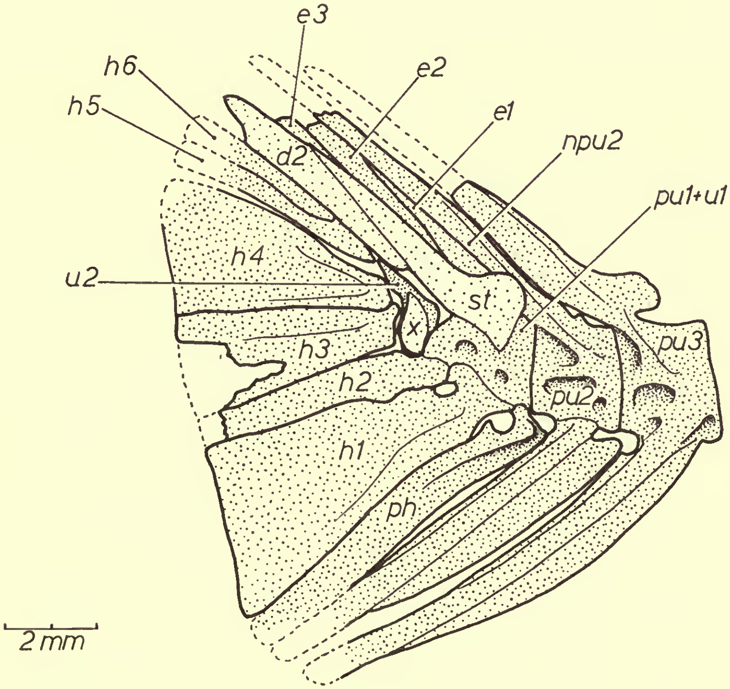


FIG. 7. *Berycopsis elegans* Dixon. Caudal skeleton of 25881, standard length *c.* 130 mm., Chalk, Sussex. *x*, unidentified plate covering second ural centrum; for explanation of other lettering see p. 102.

unsegmented caudal fin rays of *B. elegans* are soft rays, not spines as they are in *Polymixia.*

Of P.10471, a small fish lacking the head, I rashly stated that it is " certainly *B. elegans* " (Patterson 1964 : 278), but on re-examining this specimen I find that the scales are larger than in *B. elegans*, the dorsal and anal spines are longer, there are five anal spines (not four as stated earlier) and in the caudal skeleton the neural spine of the second pre-ural centrum is much reduced. This specimen is clearly not *B. elegans* and the reduced neural spine of the second pre-ural centrum shows that it is not even a polymixioid, but there is insufficient evidence to decide on its real position.

The second species of *Berycopsis*, *B. germanus* (Agassiz) from the Campanian of Westphalia, shows nothing in the caudal skeleton to distinguish it from *B. elegans* except that the haemal arch of the third pre-ural centrum is clearly autogenous and there is no sign of fusion between the third and fourth hypurals in the two specimens where this region is visible. *B. germanus* is so preserved that it shows the details of the caudal fin-rays much better than *B. elegans.* The foremost rays of the caudal fin are arranged asymmetrically, the upper rays articulating with the neural spine of the second pre-ural centrum, the lower with the haemal spine of the third pre-ural centrum. The first principal ray (unbranched) of the upper lobe is preceded by four unsegmented and one segmented ray, the lower by three unsegmented and one segmented ray. It is not possible to see whether the foremost rays are spines (as in *Polymixia*) or soft rays, as in *B. elegans* and *Omosoma.*

Genus ***OMOSOMA*** Costa (1857 : 106)

Having now had the opportunity to make a direct comparison between the holotypes of *Omosoma pulchellum* (Davis 1887) (RSM 1891.59.72) and *O. intermedium* Smith Woodward (1901) (48112) I find that the two are conspecific, the median fin counts (D V, 28–30; A III–IV, 24) being the same in both. The apparent differences in proportions of the two (Smith Woodward 1901 : 420) are due to longitudinal compression of the holotype of *O. pulchellum*, the holotype of *O. intermedium* showing the true proportions of the fish. In my earlier description of *Omosoma* (Patterson 1964 : 374) the median fin counts given for *O. pulchellum* (D IV–V, 35; A III–IV, 29) were based on distorted specimens of *O. sahelalmae. O. intermedium* is therefore a synonym of *O. pulchellum.*

None of the specimens of *Omosoma* available, belonging to *O. sahelalmae* Costa (the type species) and *O. pulchellum* (Davis), from the Upper Santonian of Sahel Alma, Lebanon (Ejel & Dubertret 1966, have recently found evidence of the precise age of these beds), has the caudal skeleton sufficiently well preserved to be illustrated, but all give a picture of a caudal skeleton which does not differ significantly from that of *Berycopsis.* The foremost rays of the caudal fin are arranged asymmetrically, those of the upper lobe articulating with the neural spine of the second pre-ural centrum, those of the lower lobe with the haemal spine of the third pre-ural centrum, just as in *B. germanus.* In both the lobes of the fin there are 4 unsegmented lepidotrichia (not spines) and two segmented rays in front of the principal rays.

It is impossible to see whether the haemal arch of the third pre-ural centrum is autogenous.

Genus *PYCNOSTERINX* Heckel (1849 : 337)

Pycnosterinx is known by four species, all from the Upper Santonian of Sahel Alma, Lebanon. Figure 8 shows the caudal skeleton of *P. russeggerii* Heckel, the type species: it is very similar to those of the other polymixiids and differs from *Polymixia* (Fig. 6) only in having the postero-ventral part of the third hypural completely ossified, so that there is no gap between the hypurals supporting the upper and lower lobes of the fin. As in *Polymixia* the neural and haemal spines are strongly inclined and the epurals slender. As in *Berycopsis* and *Omosoma*, but in contrast to *Polymixia*, the foremost caudal fin-rays are arranged asymmetrically, the upper ones articulating with the neural spine of the second pre-ural centrum, the lower with the haemal spine of the third pre-ural centrum. In both the upper and lower lobes of the fin the principal rays are preceded by three unsegmented soft rays and three segmented rays. *P. discoides* Heckel and *P. gracilis* Davis do not differ in caudal structure from *P. russeggerii* except that in *P. gracilis* there appear to be only five procurrent rays. I have seen no specimens of *P. dubius* Davis in which the caudal skeleton and fin are well preserved, but in the holotype of *Pycnosterinx latus* Davis (1887 : 534, pl. 27, fig. 2), RSM 1891.59.77 (referred to as a " fragmentary fish of indeterminable genus " by Smith Woodward 1901 : 395), the scales have the same spinous surface as in *P. dubius* (Patterson 1964 : 380) and it is probable that the specimen is a large, distorted individual of *P. dubius*, although the state of

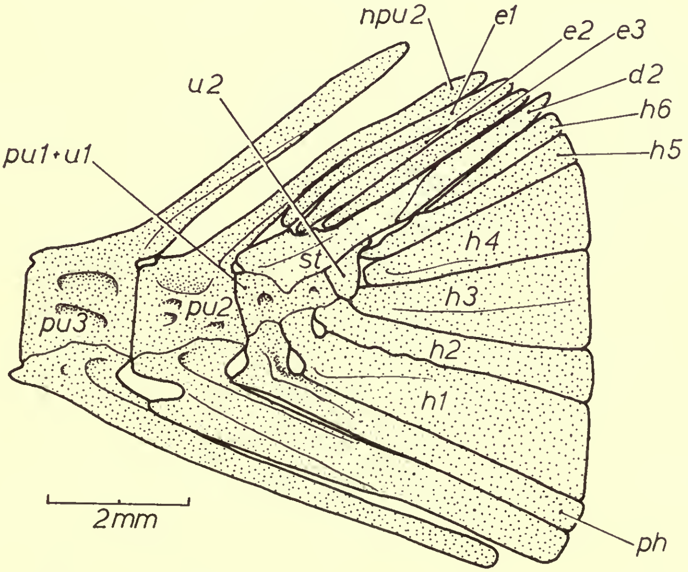


FIG. 8. *Pycnosterinx russeggerii* Heckel. Caudal skeleton of 47820, standard length 78 mm., Upper Santonian, Sahel Alma, Lebanon. For explanation of lettering see p. 102.

preservation of this and the holotype of *P. dubius* is such that this cannot be demonstrated with sufficient certainty to synonymize the two species. *P. latus* appears to have one or two more anal fin-rays and caudal vertebrae than the holotype of *P. dubius*. The caudal skeleton is completely exposed in the holotype of *P. latus* and does not differ from that of *P. russeggerii* in any way, but both in this specimen and in *P. dubius* the foremost fin-rays are true spines, a difference from the other species of *Pycnosterinx* and a resemblance to the living *Polymixia*.

Genus ***HOMONOTICHTHYS*** Whitley (1933 : 146)

All three species of this genus occur in the Upper Cenomanian—Lower Turonian of the English Chalk. In the type species, *H. dorsalis* (Dixon), only one specimen, 43575, shows anything of the caudal skeleton and here it is only possible to see that there was a fully developed neural spine on the second pre-ural centrum and that the foremost rays of the upper caudal lobe are true spines, articulating with the neural spine of the third pre-ural centrum. In these last two features *H. dorsalis*

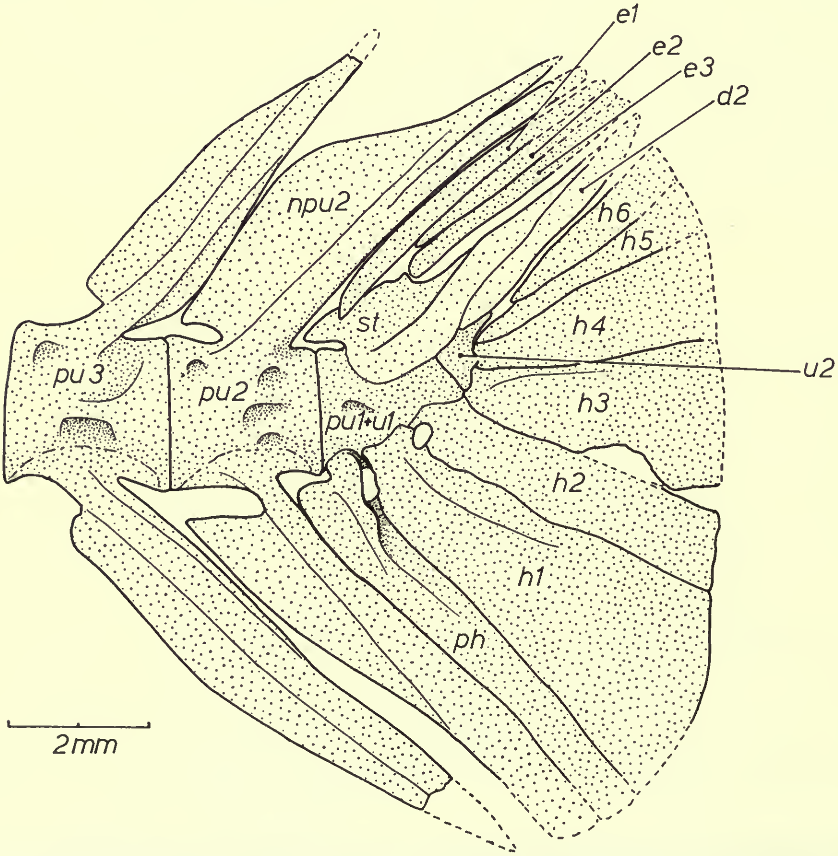


FIG. 9. *Homonotichthys pulchellus* (Dixon). Caudal skeleton of P.11112, standard length c. 110 mm., Lower Chalk, Amberley, Sussex. For explanation of lettering see p. 102.

resembles *Polymixia* and differs from other Cretaceous polymixiids except *Pycnosterinx dubius*.

In *H. pulchellus* (Dixon) the caudal skeleton is preserved in the holotype, 25886, and in two specimens only recently recognized as belonging to this species, P.11112 (Fig. 9) and P.10639: the latter are about 110 and 120 mm. respectively in standard length, the largest examples of this species yet recorded. The caudal skeleton of P.11112 (Fig. 9) is abnormal in the partial doubling of the neural spine of the second pre-ural centrum and in having the second epural smaller than the third. The caudal skeleton of *H. pulchellus* is very like that of *Polymixia*, with autogenous haemal arches on the second and third pre-ural centra (*pu2*, *pu3*) six hypurals (*h1 — 6*), three slender epurals (*e1 — 3*), a free second ural centrum (*u2*), a stegural (*st*) and a second uroneural (*d2*). The postero-ventral corner of the third hypural is truncated, but less so than in *Polymixia*. Broad flanges on the anterior margin of the neural spines of the second and third pre-ural centra are characteristic of *H. pulchellus*. All three specimens show that the foremost caudal rays are spines, as in *H. dorsalis* and *Polymixia*. In P.10639 the caudal rays articulate with the neural and haemal spines of the third pre-ural centrum, as in *Polymixia*. In P.11112 where the second pre-ural spine is abnormal, the foremost upper caudal rays articulate with the neural spine of the second pre-ural centrum. The lowermost principal caudal ray (unbranched) is preceded by four spines and three segmented rays. P.11112 shows the anal fin of *H. pulchellus*, previously unknown. The fin contains five spines, the first very small and the fifth the longest and thickest, and about eleven soft rays. The fifth anal spine is equal in length to the longest dorsal spine, just over one-quarter of the maximum depth of the trunk.

H. rotundus (Smith Woodward) is known only by the holotype, P.315, and P.5682. P.5682 shows most of the details of the caudal skeleton: there is nothing to distinguish it from the other polymixiids described here except that there is no flange on the anterior margin of the neural spine of the second pre-ural centrum as there is in *H. pulchellus*. P.315 shows that the foremost caudal rays are soft rays, longitudinally divided, not spines as they are in *H. dorsalis*, *H. pulchellus* and *Polymixia*. These two points may be added to others (Patterson 1964 : 299) indicating that this species is incorrectly placed in *Homonotichthys*, but more specimens are necessary before its true position can be decided.

Family **SPHENOCEPHALIDAE** Patterson (1964 : 383)

The only member of this family is *Sphenocephalus fissicaudus* Agassiz from the Campanian of Westphalia. Of the six specimens in the British Museum (Natural History), three, P.2100 (Fig. 10), P.8772 and P.9059 have the caudal skeleton well preserved. As in Polymixiidae, the second pre-ural centrum has a fully developed neural spine (*npu2*), there is a free second ural centrum (*u2*), a stegural (*st*), a second uroneural (*d2*), and six hypurals (*h1 — 6*). As in *Polymixia*, the foremost procurrent rays articulate with the neural and haemal spines of the third pre-ural centrum. In contrast to all Polymixiidae there are only two epurals (*e1*, *2*), the first curved forwards proximally and with a gap between it and the neural spine of the second

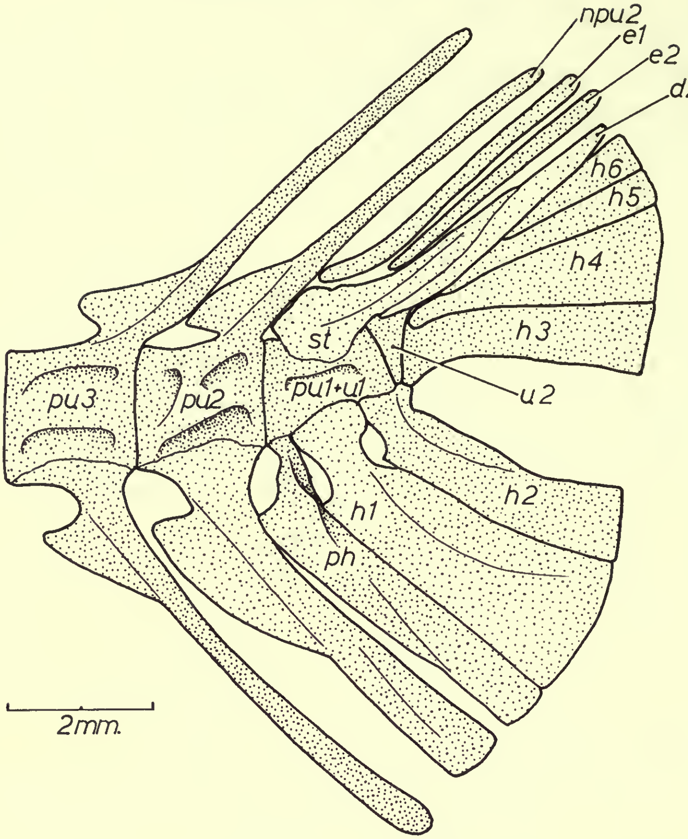


FIG. 10. *Sphenocephalus fissicaudus* Agassiz. Caudal skeleton of P.2100, standard length 92 mm., Campanian, Sendenhorst, Westphalia. For explanation of lettering see p. 102.

pre-ural centrum, there is a wide gap between the upper and lower hypurals, and there is a large number of procurrent rays, apparently nine in each lobe, six unsegmented soft rays and three segmented in the upper, five unsegmented and four segmented in the lower.

Suborder DINOPTERYGOIDEI Patterson (1964 : 434)

This suborder contains four monotypic Uppper Cretaceous familes, probably not closely related. As the caudal skeleton in the type family, the Dinopterygidae, is poorly known, the best known family, the Aipichthyidae, will be described first.

Family **AIPICHTHYIDAE** Patterson (1964 : 303)

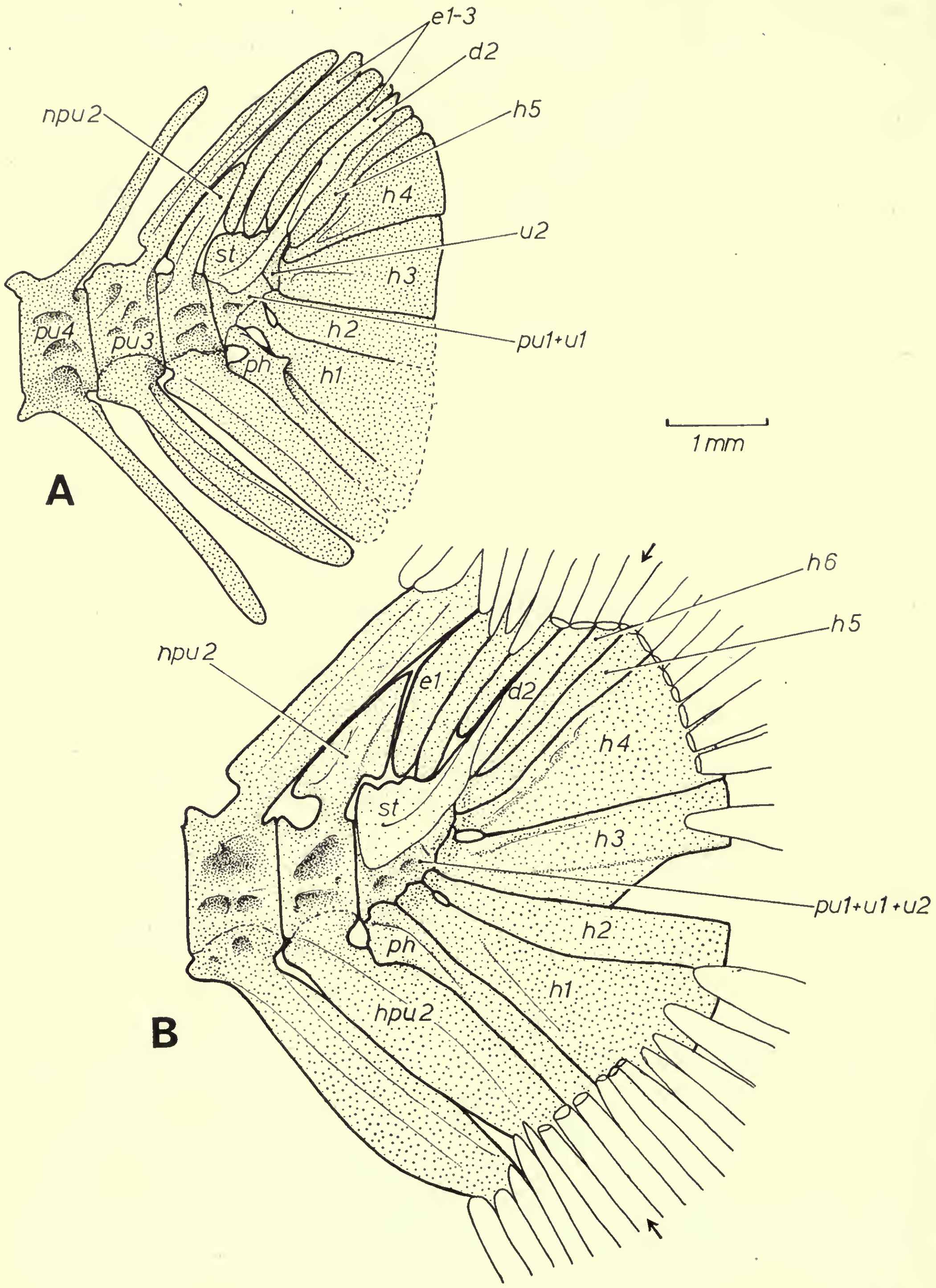
Genus ***AIPICHTHYS*** Steindachner (1860 : 763)

I have seen no material of the type species, *A. pretiosus* Steindachner from the Lower Cenomanian of Dalmatia, and the caudal region is not preserved in *A.*

nuchalis (Dixon) from the English Chalk. The other two species, *A. minor* (Pictet) and *A. velifer* Smith Woodward, both from the Cenomanian of Hakel, Lebanon, are well represented in the British Museum (Natural History). They show a remarkable range of variation in the structure of the caudal skeleton. In most specimens of *Aipichthys* the distal parts of the hypurals, epurals and uroneurals are obscured by the deeply cleft bases of the caudal fin-rays, but in P.82 (*A. minor*, Fig. 11A) the fin-rays are displaced, exposing these bones. In this specimen and in all others the neural and haemal spines of the third pre-ural centrum (*pu3*) are broad and elongate and the first procurrent rays of the fin articulate with them. The haemal arches of the second and third pre-ural centra are autogenous. In contrast to all Polymixioidei, the neural spine of the second pre-ural centrum (*npu2*) is normally only about half as long as its predecessor, which makes contact with the first epural distally. Though somewhat expanded, this neural spine is more like those of *Elops* (Nybelin 1963, figs. 1, 4) and *Nematonotus* (Fig. 25) than the shorter, broader spine in *Aulolepis* and *Ctenothrissa* (Figs. 2, 4, 5): it does not resemble the very low crest on this centrum in Berycoidei and percoids. In one specimen of *Aipichthys minor*, P.6183 (Fig. 11C), the neural spine of the second pre-ural centrum is fully developed and supports epaxial fin-rays, as in Polymixioidei. This is clearly an individual variation, comparable to those found in certain individuals of *Monocentris* (Fig. 14) and *Siniperca* (Fig. 26), and is recognizable as such by the gap between the spine and the proximal part of the first epural, which is filled by flanges from the posterior face of the spine and from the anterior face of the epural. In all specimens of *Aipichthys* there are three epurals (*e1 — 3*) and the first ural and pre-ural centra are fused (*pu1 + u1*). There is normally a free second ural centrum (*u2*, Figs. 11A, C), but in occasional individuals, like the large specimen shown in Fig. 11B, the second ural centrum is fused into the preceding compound centrum (*pu1 + u1 + u2*), although the line of fusion is visible in transparency under xylene. There is always a stegural (*st*) and a second uroneural (*d2*). In *A. minor* there are normally six hypurals (*h1 — 6*, Figs. 11B, C), as in Polymixioidei, but in P.82 (Fig. 11A) the fifth hypural is partially divided distally suggesting that the sixth is fused into it. In all specimens of *A. velifer* in which the hypurals are visible (P.4743, P.4744, 49486, P.47862) there appear to be only five hypurals. Preceding the principal rays of the caudal fin there are four unsegmented soft rays and three segmented rays in the upper lobe, three unsegmented and three segmented rays in the lower.

Family **PHARMACICHTHYIDAE** Patterson (1964 : 398)

This family contains only *Pharmacichthys venenifer* Smith Woodward (1942) from the Middle Cenomanian of Hakel, Lebanon. None of the five known specimens of this species has the caudal skeleton sufficiently well preserved to be illustrated, but the holotype, AUB 104691/99, and AUB 101872 show most of the caudal anatomy. The suggestion (Patterson 1964 : 401) that the nearest relative of *Pharmacichthys* is *Aipichthys* is borne out by the structure of the caudal skeleton and fin. In almost every respect the caudal skeleton of *Pharmacichthys* is identical with that of *Aipichthys* (Fig. 11). The foremost caudal fin-rays articulate with the neural and haemal


e1-3
d2
npu2
h5
h4
u2
st
h3
pu1+u1
h2
pu4
pu3
ph
h1
A
1 mm
h6
npu2
h5
e1
d2
h4
st
h3
pu1+u1+u2
h2
ph
h1
hpu2
B

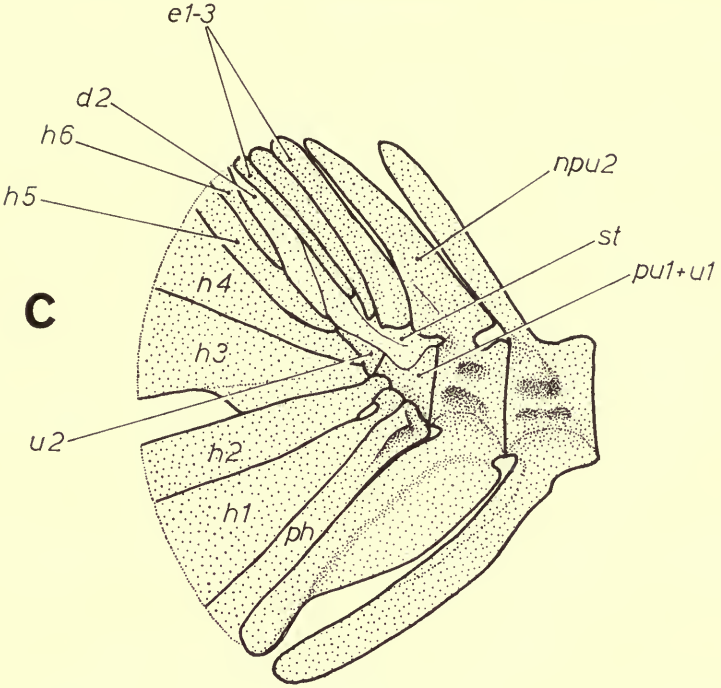


Fig. 11. *Aipichthys minor* (Pictet). Caudal skeleton of **A**, P.82, standard length 32 mm.; **B**, RSM 1881.5.41, standard length *c.* 50 mm.; **C**, P.6183, standard length 36 mm. All from Middle Cenomanian, Hakel, Lebanon. For explanation of lettering see p. 102. In **B** arrows mark the outermost (unbranched) principal fin-rays.

spines of the third pre-ural centrum, the neural spine of the second pre-ural centrum is about half as long as its predecessor, as in *Aipichthys*, the haemal spine of the second pre-ural centrum has a broad flange on its anterior edge, there are three epurals and the principal rays of the fin are preceded by four unsegmented soft rays and three segmented rays above, three unsegmented and three segmented rays below. It is impossible to see whether there are five or six hypurals. A further resemblance to *Aipichthys*, not previously noticed, is that the bases of the caudal rays are deeply cleft, overlapping much of the hypurals (" hypurostegy ", Le Danois & Le Danois 1964). The only difference from *Aipichthys*, suggested by the holotype, AUB 101872 and AUB 102601, is that the first and second hypurals appear to be fused.

Family PYCNOSTEROIDIDAE Patterson (1964 : 389)

The only member of this family is *Pycnosteroides levispinosus* (Hay 1903) from the Middle Cenomanian of Hajula, Lebanon. The caudal skeleton and fin are present in two specimens, P.13900 (Fig. 12) and AMNH 4519*a* (Hay 1903, pl. 32, fig. 3). *Pycnosteroides* differs from *Aipichthys* and *Pharmacichthys* in having the foremost rays of the caudal fin inserted on the first epural above and the haemal spine of the third pre-ural centrum below, and in having a fully developed neural spine on

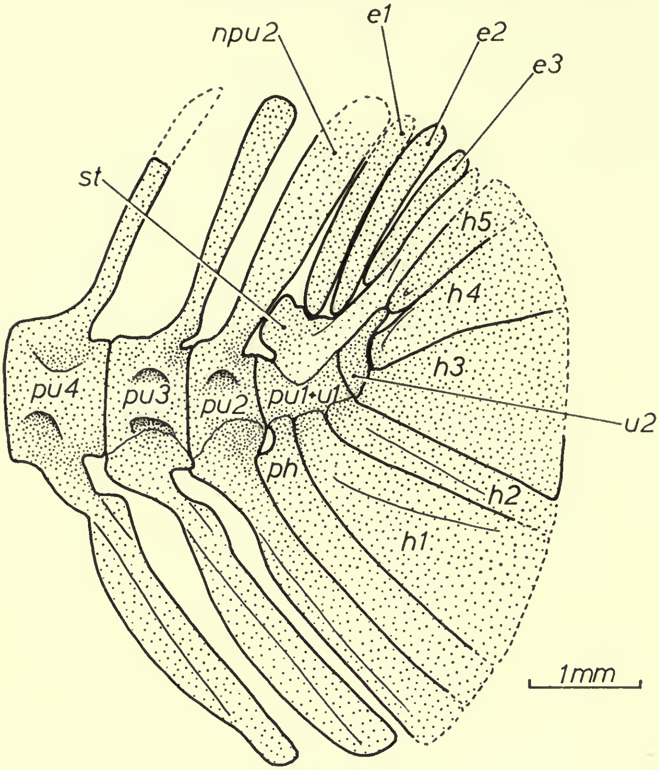


FIG. 12. *Pycnosteroides levispinosus* (Hay). Caudal skeleton of P.13900, standard length *c.* 50 mm., Middle Cenomanian, Hajula, Lebanon. For explanation of lettering see p. 102.

the second pre-ural centrum (*npu2*). This neural spine differs from those of the Polymixioidei in being expanded distally. The haemal arches of the second and third pre-ural centra (*pu2*, *pu3*) are autogenous. In the fusion of the first ural and first pre-ural centra (*pu1* + *u1*), the free second ural centrum (*u2*), and the form of the stegural (*st*) and second uroneural (missing in the figured specimen but present in AMNH 4519*a*) *Pycnosteroides* agrees with *Aipichthys* and the Polymixioidei. There are three epurals (*e1* — *3*). In P.13900, as in *Aipichthys velifer*, there are only five hypurals (*h1* — *5*), but here the first and third are the largest, the third being much larger than the fourth. In AMNH 4519*a* there are six hypurals. In contrast to *Aipichthys* and *Pharmacichthys* there are only three soft rays, all unsegmented, in front of both the upper and lower principal rays, and the fin-rays are not deeply cleft basally.

Family **DINOPTERYGIDAE** Jordan (1923 : 173)

This family, the type of the suborder, contains only *Dinopteryx spinosus* (Davis) from the Upper Santonian of Sahel Alma, Lebanon.

The caudal region is very imperfectly preserved in the holotype, 46536/P.4761, but is more or less completely visible in USNM 22217 and 22219. As in other respects (Patterson 1964 : 392), *Dinopteryx* resembles *Pycnosteroides* in the caudal skeleton. The second pre-ural centrum has a fully developed neural spine and both this and the preceding neural spine are expanded distally, as in *Pycnosteroides* (Fig. 12). As in *Pycnosteroides* there are three epurals, the first ural and pre-ural centra are fused, there is a free second ural centrum, a stegural and a second uroneural. USNM 22219 shows that there were at least three upper hypurals, shaped as in *Pycnosteroides*, but it is impossible to be certain whether or not a small sixth hypural was present. The foremost procurrent caudal rays articulate with the neural spine of the second pre-ural centrum above and the haemal spine of the third pre-ural centrum below, further forwards than in *Pycnosteroides*. There are four spines and two segmented rays in front of the principal rays above, three spines and two segmented rays below, both the holotype and USNM 22217 showing that the foremost procurrent rays were true spines, a difference from other Dinopterygoidei.

Suborder BERYCOIDEI Patterson (1964 : 433)

This suborder, containing eight living families, is represented in the Cretaceous only by two families, the Trachichthyidae and Holocentridae. A detailed discussion of the relationships between these two families in the Cretaceous will be found in

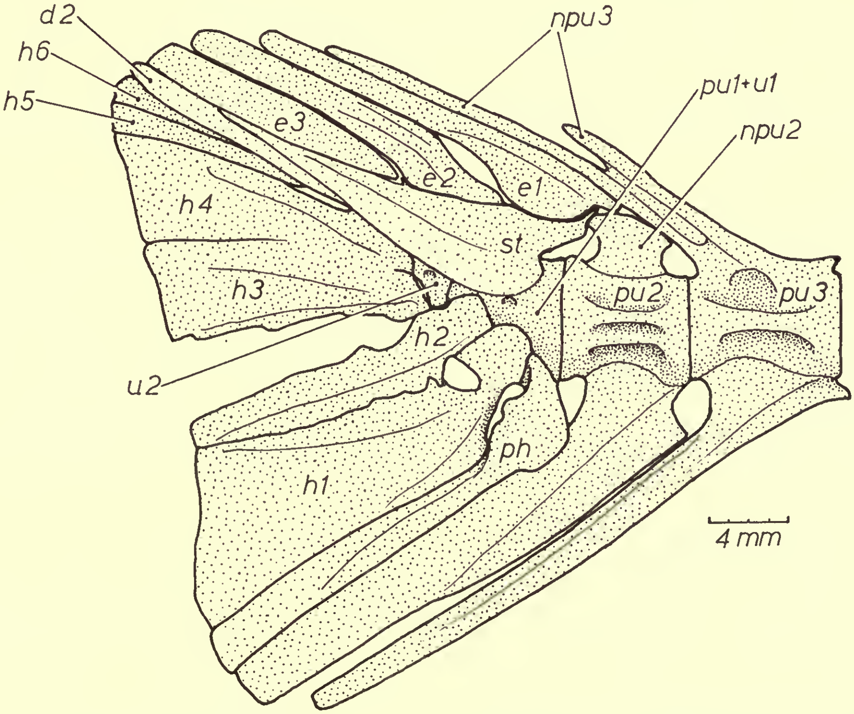


FIG. 13. *Hoplostethus mediterraneus* Cuvier & Valenciennes. Caudal skeleton of a dried skeleton, 1878.4.5.8, standard length 190 mm., Japan. For explanation of lettering see p. 102.

Patterson (1967). Among living Berycoidei, the caudal skeleton of *Centroberyx affinis* (Berycidae) has been illustrated by Regan (1911, fig. 2), those of *Hoplostethus* (Trachichthyidae), *Holocentrus* and *Myripristis* (both Holocentridae) are briefly discussed by Gosline (1961 : 14) and a caudal skeleton of *Holocentrus ascensionis* is figured by Rosen (1964, fig. 23D). Fig. 13 shows the caudal skeleton of the living *Hoplostethus mediterraneus* (Trachichthyidae). In most respects this is typical of primitive Berycoidei, with autogenous haemal spines on the second and third pre-ural centra, the second pre-ural centrum without a neural spine, bearing only a low, broad crest (*npu2*) which lies *below* the proximal end of the first epural, three epurals (*e1 — 3*), six hypurals (*h1 — 6*), a free second ural centrum (*u2*), a stegural (*st*) and a second uroneural (*d2*). In the specimen illustrated the neural spine of the third pre-ural centrum (*npu3*) is double distally and the third and fourth hypurals are fused proximally: these features are individual abnormalities. The neural crest on the second pre-ural centrum is autogenous—this is a primitive feature which also occurs in primitive myctophoids (*Nematonotus* and *Aulopus*, p. 81). In *Hoplostethus* the foremost procurrent fin-rays articulate with the neural and haemal spines of the third pre-ural centrum. In living trachichthyids (*Hoplostethus, Trachichthys, Paratrachichthys, Gephyroberyx*) the nineteen principal caudal rays are normally preceded by six spines and one segmented ray above and below.

The caudal skeleton in living holocentrids is described below (p. 75, Fig. 20). In Berycidae (Regan 1911, fig. 2) the caudal skeleton is advanced over the trachichthyid condition in having both the second ural centrum and the stegural fused into the compound first ural and pre-ural centrum. Nothing is known of the caudal skeleton in Korsogasteridae and Anomalopidae. Dissection of single specimens of *Diretmus* (Diretmidae) and *Anoplogaster* (Anoplogasteridae) shows that both resemble Berycidae in having the stegural and second ural centrum fused into the preceding compound centrum, while in *Anoplogaster* the second uroneural is lost and in *Diretmus* the sixth hypural is lost and there is fusion between the first and second hypurals and between the third and fourth hypurals. In the Stephanoberycoidei, which appear to be only specialized derivatives of the Berycoidei, *Gibberichthys* (Gibberichthyidae) agrees with trachichthyids such as *Hoplostethus* in the caudal skeleton but *Melamphaes* (Melamphaeidae) has both the stegural and second ural centrum fused with the preceding centrum, a much reduced second uroneural, only five hypurals and fusion within the upper and lower hypurals. All living berycoids and stephanoberycoids seem to be characterized by the presence of spinous procurrent caudal rays.

In *Monocentris* (Monocentridae) the caudal skeleton normally shows the same major features as the figured specimen of *Hoplostethus* (even to the partial doubling of the neural spine of the third pre-ural centrum), but in one of the available skeletons (Fig. 14) there is a fully developed neural spine on the second pre-ural centrum (*npu2*) and the neural spine of the third pre-ural centrum is single. There are three epurals (*e1–3*), so that in this individual the neural spine on the second pre-ural centrum has apparently developed instead of the normal doubling of the neural spine of the preceding centrum. The caudal skeleton of this specimen resembles those of polymixioids and the dinopterygoids *Pycnosteroides* and *Dinopteryx*, but

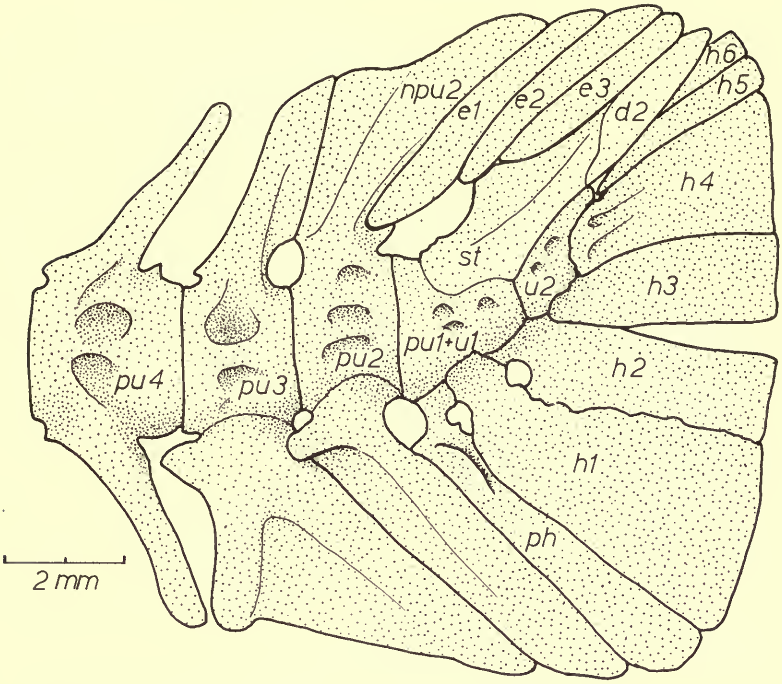


FIG. 14. *Monocentris japonicus* (Houttuyn). Caudal skeleton of a dried skeleton showing a neural spine on the second pre-ural centrum, 1862.11.1.47, standard length 125 mm., Japan. For explanation of lettering see p. 102.

it is questionable whether this is significant. However, *Monocentris* seems to be the only living berycoid in which the procurrent caudal rays are sometimes not spines but unsegmented soft rays: of four specimens examined, one has no spines and one has only one spine in front of the lower caudal lobe and none above. *Monocentris* is a fish of highly specialized appearance and the skull suggests that the Monocentridae are derivatives of the Trachichthyidae, but there is a patch of teeth on the endopterygoid (Starks 1904 : 618), a character otherwise unknown in Berycoidei, and this and the occasional absence of procurrent caudal spines suggest that the Monocentridae may have had a long independent history.

Family **TRACHICHTHYIDAE** Bleeker (1859)

The caudal skeleton of the living *Hoplostethus mediterraneus* is described above (Fig. 13).

Genus ***HOPLOPTERYX*** Agassiz (1838 : 4)

Hoplopteryx, with eight species ranging from the Middle Cenomanian to the Upper Senonian, is the longest-ranging and largest genus of Cretaceous Trachichthyidae.

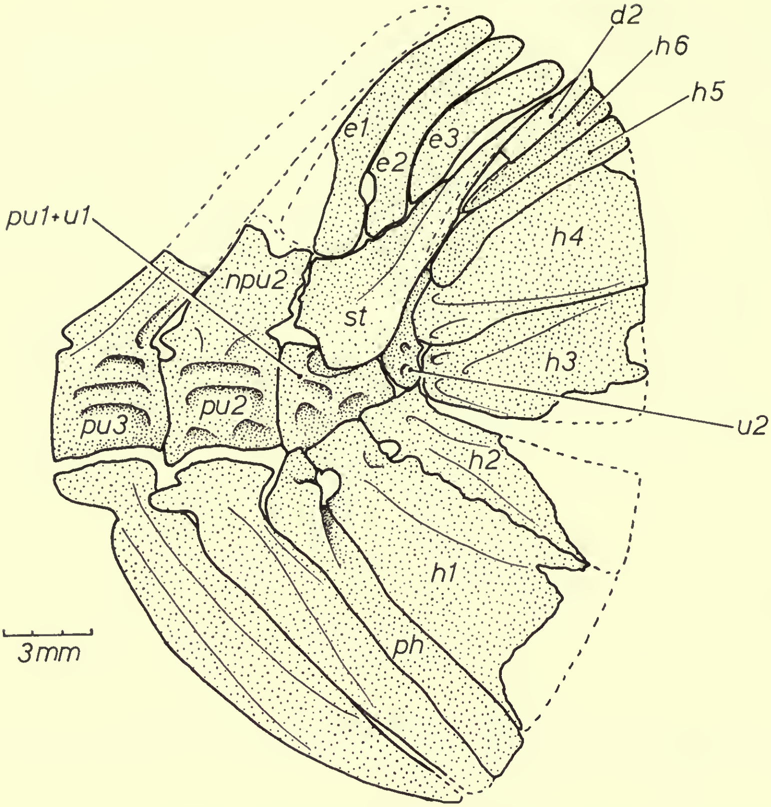


Fig. 15. *Hoplopteryx lewesiensis* (Mantell). Caudal skeleton of P.1948*b*, standard length *c.* 175 mm., Chalk, Sussex. For explanation of lettering see p. 102.

In the type species, *H. antiquus* Agassiz from the Campanian of Westphalia, I have seen no specimens in which the caudal skeleton is preserved. The best known species is *H. lewesiensis* (Mantell) which ranges throughout the English Chalk: several specimens show the caudal skeleton (Figs 15, 16) which is almost identical with that of the living *Hoplostethus* (Fig. 13), with the neural arch of the second pre-ural centrum (*npu2*) reduced (though not so much as in *Hoplostethus*), the haemal arches of the second and third pre-ural centra autogenous, three epurals (*e1–3*) of which the first is especially large, a stegural (*st*) and a second uroneural (*d2*), a free second ural centrum (*u2*) and six hypurals (*h1–6*), the uppermost very small. The neural arch of the second pre-ural centrum is not autogenous as it is in *Hoplostethus*. The foremost caudal fin-rays are inserted on the first epural above and on the haemal spine of the third pre-ural centrum below. There are only three spines and one segmented ray in front of the upper principal rays and two spines and one segmented ray in front of the lower.

The other species of *Hoplopteryx* in the English Chalk are *H. simus* Smith Woodward, *H. macracanthus* Patterson and *H. gephyrognathus* Patterson. The caudal

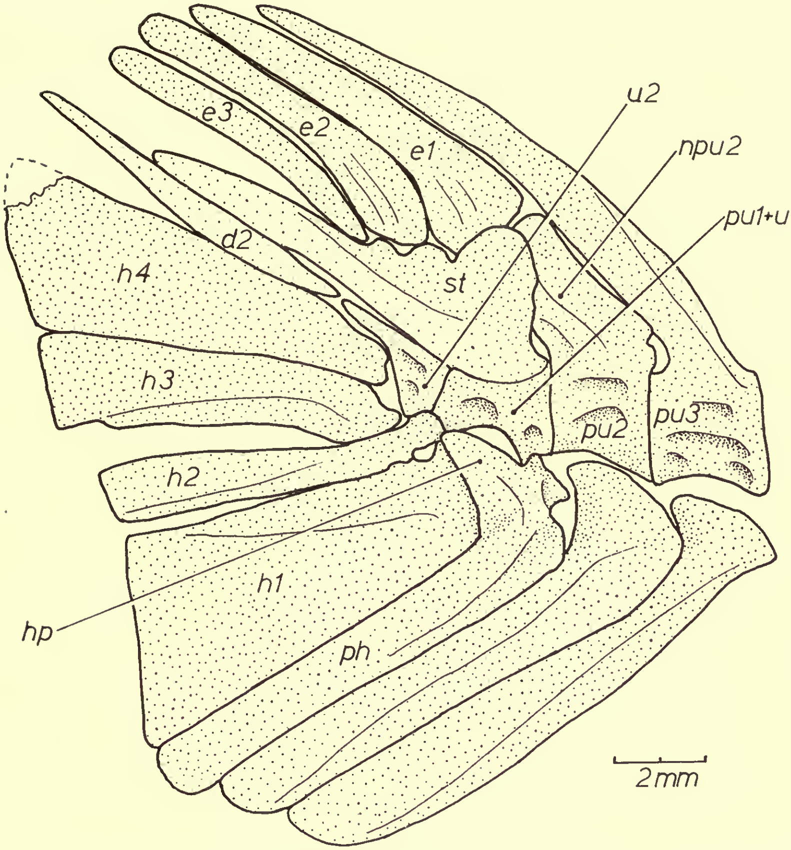


FIG. 16. *Hoplopteryx lewesiensis* (Mantell). Caudal skeleton of P.5421, standard length c. 135 mm., Lower Chalk, Lewes, Sussex. For explanation of lettering see p. 102. The second uroneural is displaced ventrally and the fifth and sixth hypurals are missing.

skeleton of *H. simus* is exposed in P.11202, that of *H. macracanthus* in P.30186: neither appears to differ from *H. lewesiensis* in any way. The caudal region is not preserved in the two known specimens of *H. gephyrognathus*.

The earliest species of *Hoplopteryx* is *H. lewisi* (Davis) from the Middle Cenomanian of Hakel, Lebanon. In this species the caudal skeleton and fin are exposed in P.10709 and partially shown in the holotype, P.4758. *H. lewisi* seems to agree with *H. lewesiensis* in every detail, even to the insertion of the foremost upper fin rays on the first epural, except that there are four spines and one segmented ray in front of the upper principal rays, three spines and one segmented ray in front of the lower.

The remaining two species of *Hoplopteryx*, *H. syriacus* (Pictet & Humbert) and *H. spinulosus* Smith Woodward, are from the Upper Santonian of Sahel Alma, Lebanon. In *H. spinulosus* I have seen no specimen in which the caudal skeleton is preserved. In *H. syriacus* parts of the caudal skeleton are preserved in 49553 and they show nothing to distinguish the species from *H. lewesiensis*.

Genus ***LISSOBERYX*** Patterson (1967 : 73)

The type species, *L. dayi* (Smith Woodward 1942), is from the M. Cenomanian of Hakel and Hajula, Lebanon. I have briefly described the caudal skeleton (Patterson 1967 : 78) which is preserved in AUB 108926 (Fig. 17) and AUB 101997. The caudal skeleton agrees well with those of *Hoplostethus* (Fig. 13) and *Hoplopteryx* (Figs 15, 16). The neural spine of the second pre-ural centrum (*npu2*) is reduced to about the same extent as in *Hoplopteryx*, there are three epurals (*e1–3*), the first long and closely applied distally to the neural spine of the third pre-ural centrum, a stegural (*st*) and a second uroneural (*d2*), and six hypurals (*h1–6*). The only significant differences from *Hoplopteryx* and *Hoplostethus* are that the fused first ural and pre-ural centrum is longer, with clear signs in the surface sculpture of its origin from two centra, and that the second ural centrum is also longer, so that the caudal skeleton appears more upturned. As in *Hoplopteryx* the foremost caudal rays articulate with the first epural above and the haemal spine of the third pre-ural centrum below. The principal rays are preceded by four spines and one unsegmented ray above, three spines and one segmented ray below.

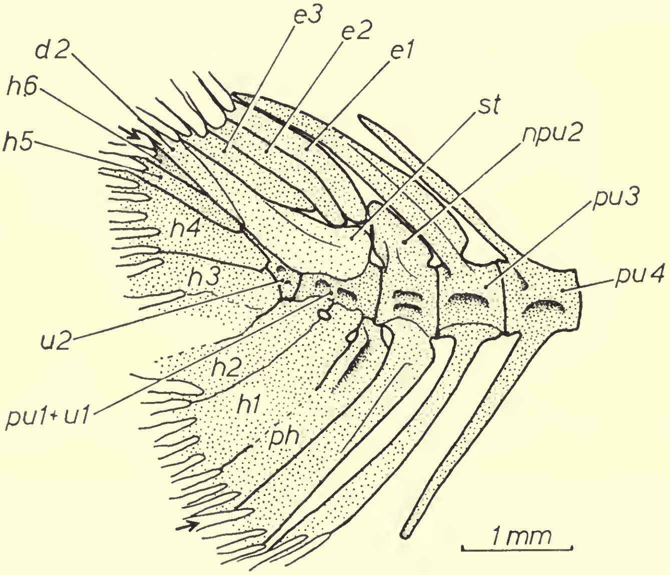


FIG. 17. *Lissoberyx dayi* (Smith Woodward). Caudal skeleton of AUB 108926, standard length 34 mm., Middle Cenomanian, Hajula, Lebanon. For explanation of lettering see p. 102. Arrows mark the outermost (unbranched) principal fin-rays.

Genus ***ACROGASTER*** Agassiz (1838 : 5)

I have seen no specimens of *A. parvus* Agassiz, the type species, or of *A. brevicostatus* von der Marck, both these species from the Campanian of Westphalia being poorly known. The remaining species, *A. heckeli* (Pictet) and *A. daviesi* (Davis), from the Upper Santonian of Sahel Alma, Lebanon, are common and several specimens in the British Museum (Natural History) show the caudal skeleton clearly: I can find no differences between these two species in caudal anatomy. A specimen of *A. heckeli* is illustrated in Fig. 18. As in the other trachichthyids described above, the neural spine of the second pre-ural centrum is reduced (*npu2*), there are three epurals (*e1–3*), a stegural (*st*), a second uroneural (*d2*) and six hypurals (*h1–6*). The fused first ural and pre-ural centra (*pu1* + *u1*) and the second ural centrum (*u2*) are elongate, as in *Lissoberyx*, and the caudal skeleton appears strongly upturned. As in *Hoplopteryx* and *Lissoberyx*, the foremost caudal rays articulate with the first epural above and the haemal spine of the third pre-ural centrum below. The principal caudal rays are preceded by four or five spines and one segmented ray above, three or four spines and one segmented ray below.

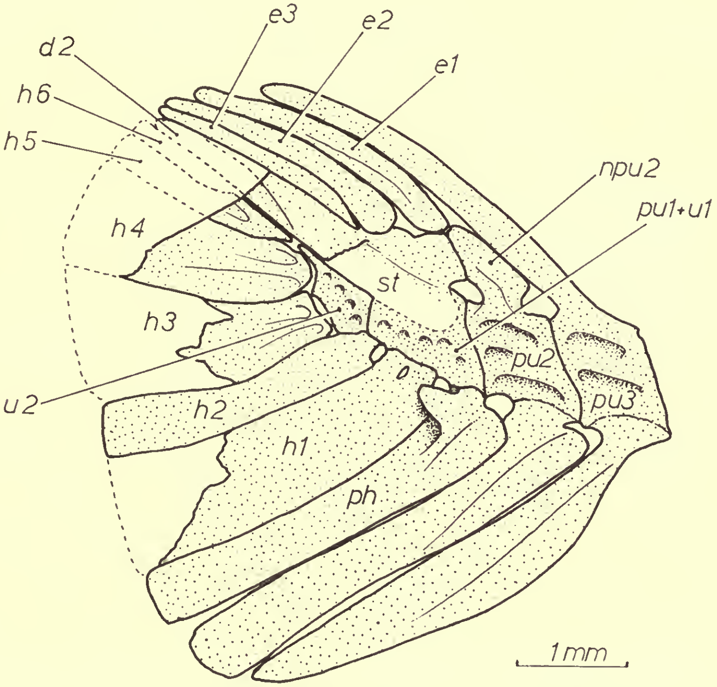


FIG. 18. *Acrogaster heckeli* (Pictet). Caudal skeleton of P.4155, standard length *c.* 55 mm., Upper Santonian, Sahel Alma, Lebanon. For explanation of lettering see p. 102.

Genus *TUBANTIA* Patterson (1964 : 413)

The only species is *T. cataphractus* (von der Marck), from the Campanian of Westphalia, in which the caudal skeleton is well exposed in P.21984 (Fig. 19). *Tubantia* agrees with other trachichthyids in the reduction of the neural spine of the second pre-ural centrum (*npu2*), the three epurals (*e1–3*), stegural (*st*), second uroneural (*d2*), and six hypurals (*h1–6*). As in *Hoplostethus*, the fused first ural and pre-ural centrum (*pu1 + u1*) is only as long as the preceding centrum. *Tubantia* differs from other Cretaceous trachichthyids and resembles living forms in having the number of procurrent rays increased to nine spines and two segmented rays above, six spines and two segmented rays below, these small rays extending forwards in front of the tips of the neural and haemal spines of the third pre-ural centrum.

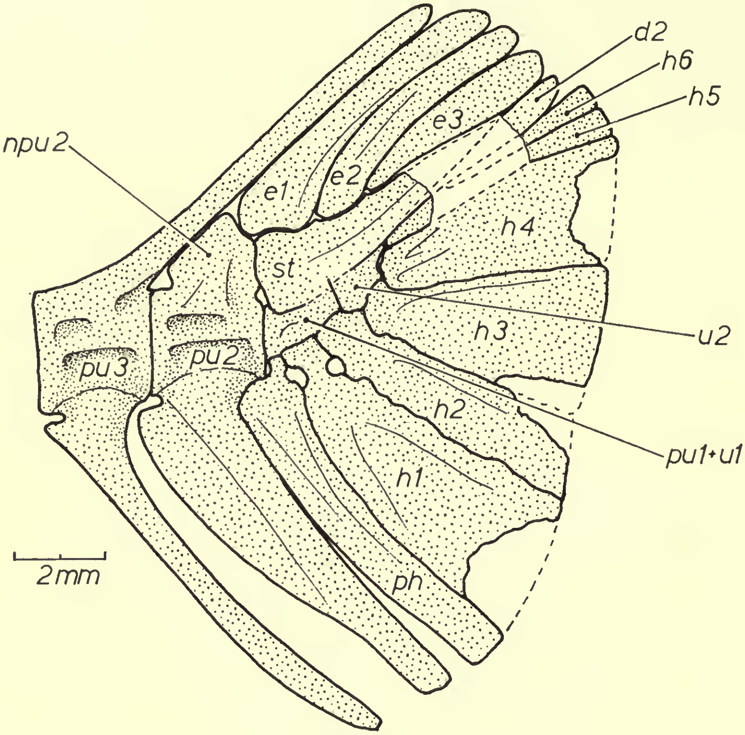


Fig. 19. *Tubantia cataphractus* (von der Marck). Caudal skeleton of P.21984, standard length 130 mm., Campanian, Baumberg, Westphalia. For explanation of lettering see p. 102.

Genus *GNATHOBERYX* Patterson (1967 : 81)

The type and only species, *G. stigmosus* Patterson (1967 : 82), from the Upper Santonian of Sahel Alma, Lebanon, is known by two specimens and the caudal skeleton is preserved only in the holotype, AUB 100402, where it is compressed and distorted. So far as can be seen, the caudal skeleton and fin agree with other Cretaceous trachichthyids such as *Lissoberyx*, *Hoplopteryx* and *Acrogaster*, with the neural spine of the second pre-ural centrum reduced, the stegural free, a free second ural centrum, and the upper principal rays preceded by four spines and one segmented ray, the foremost articulating with the first epural.

Family **HOLOCENTRIDAE** Richardson (1846)

The caudal skeleton of the living *Myripristis adustus* is shown in Fig. 20: it shows no significant differences from those of several species of *Holocentrus*. The neural and haemal spines of the fourth (*pu4*) and fifth pre-ural centra are expanded but short. The neural spine of the second pre-ural centrum (*npu2*) is greatly reduced (and not autogenous as it is in *Hoplostethus*), with the tip of the first epural lying above it. The haemal arches of the second and third pre-ural centra (*pu2*, *pu3*) are autogenous and there are three epurals (*e1–3*). In contrast to the trachichthyids the two ural centra, the first pre-ural centrum and the stegural are all fused into a single structure (*pu1* + *u1* + *u2* + *st*) and there are only five hypurals (*h1–5*) the uppermost hypural present in trachichthyids having been lost. The second uroneural (*d2*) is free and fits proximally into a notch in the stegural rather than lying below and behind it. In *Myripristis* the foremost caudal rays articulate with the first epural above (as in most Cretaceous trachichthyids) and with the haemal

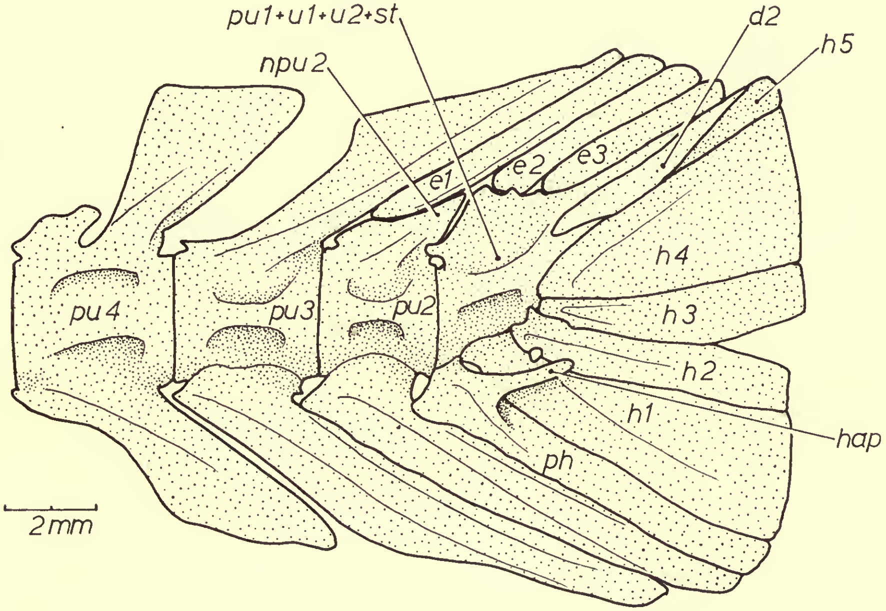


Fig. 20. *Myripristis adustus* Bleeker. Caudal skeleton of a dried skeleton, 1858.4.21.239, standard length 155 mm., Amboina. *hap*, hypurapophysis; for explanation of other lettering see p. 102.

spine of the third pre-ural centrum below. In *Holocentrus* the foremost rays articulate with the neural and haemal spine of the third pre-ural centrum. In *Myripristis* the principal caudal rays are preceded by four spines and one segmented ray above and below. Rosen (1964, fig. 23D) has figured a caudal skeleton of *Holocentrus ascensionis* which differs from all the Recent holocentrid skeletons that I have seen in having a free second ural centrum. Rosen does not say how large his specimen was, but if it was an alizarin-stained juvenile this difference can be explained.

Genus ***CAPROBERYX*** Regan (1911 : 8)

In the type species, *C. superbus* (Dixon) from the Turonian of the English Chalk, the caudal skeleton is exposed in P.3979 (Fig. 21). The neural and haemal spines of the fourth (*pu4*) and fifth pre-ural centra are normal, not expanded as in living holocentrids. The haemal arches of the second and third pre-ural centra (*pu2*, *pu3*) are autogenous, the neural spine of the second pre-ural centrum (*npu2*) is reduced and there are three epurals (*e1–3*), all as in living holocentrids. In contrast to living holocentrids, the stegural (*st*) is not fused to the underlying centrum (*pu1* + *u1*) and the second ural centrum (*u2*) is free. The second uroneural (*d2*) is fused to the stegural (*st*) distally, but this is perhaps only a consequence of the very large size (standard length *c.* 40 cm) of this specimen. As in living holocentrids there are only five hypurals, but the distribution of the branched principal fin-rays (one on

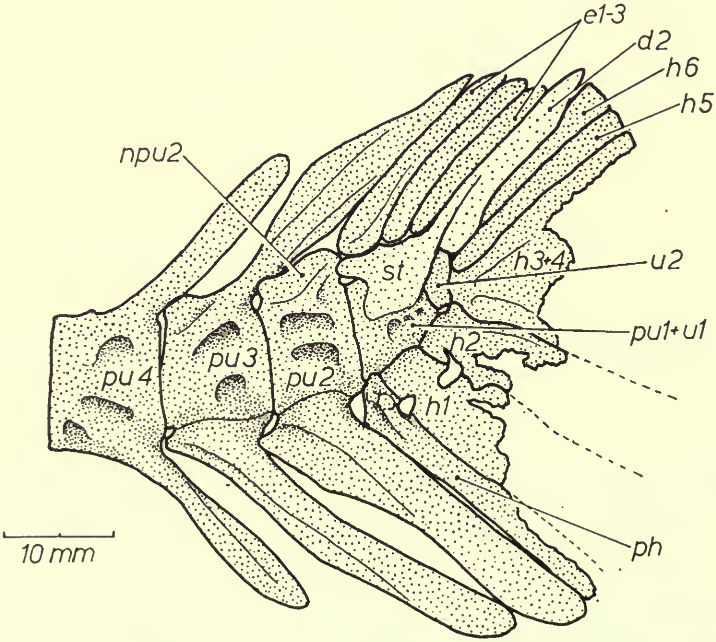


Fig. 21. *Caproberyx superbus* (Dixon). Caudal skeleton of P.3979, standard length *c.* 400 mm., Chalk, Sussex. For explanation of lettering see p. 102.

the uppermost hypural, two on the one below and six on the next) shows that the three upper hypurals are the third and fourth fused (*h3 + 4*), the fifth (*h5*) and the sixth (*h6*), for in living holocentrids the three upper hypurals, the third, fourth and fifth, bear two, six and one branched principal rays respectively. *Caproberyx* therefore agrees with the trachichthyids in retaining the small sixth hypural, and the fusion of the third and fourth hypurals shown by P.3979 is again probably merely a consequence of the large size of the fish. As in *Myripristis* and most Cretaceous trachichthyids, the foremost caudal fin-rays articulate with the first epural above and the haemal spine of the third pre-ural centrum below, and there are probably four spines and one segmented ray in front of the principal caudal rays above and below. Characters of the skull and fins suggest that *Caproberyx* is the most primitive holocentrid known, lying near to the common stock of the Holocentridae and Trachichthyidae (Patterson 1964 : 359; 1967 : 103). This is confirmed by the structure of the caudal skeleton in *C. superbus*, for in the six hypurals, the free stegural and second ural centrum, and the unexpanded neural and haemal spines of the posterior caudal vertebrae, this species resembles the trachichthyids rather than other holocentrids.

The other species of *Caproberyx* are *C. polydesmus* (Arambourg 1954) from the Lower Cenomanian of Jebel Tselfat, Morocco, and *C. pharsus* Patterson (1967 : 97) from the Middle Cenomanian of Hakel, Lebanon. *C. pharsus* is known only by a specimen lacking the caudal region. *C. polydesmus* is known only by the holotype: Arambourg's figure (1954, pl. 19, fig. 1) shows that the neural and haemal spines of the fourth and fifth pre-ural centra are not expanded, as in *C. superbus*, and he described the principal rays as having five or six small rays in front of them in each lobe.

Genus ***STICHOCENTRUS*** Patterson (1967 : 88)

The type and only species is *S. liratus* Patterson from the Middle Cenomanian of Hajula, Lebanon. The caudal skeleton is well preserved in AUB 108923 (Fig. 22) and is partially shown in AUB 108927 and 108929. The neural and haemal spines of the fifth pre-ural centrum are unmodified but those of the fourth (*pu4*) are expanded, though not so strongly as in living holocentrids. The autogenous haemal arches on the second and third pre-ural centra, the reduced neural spine on the second pre-ural centrum (*npu2*) and the three epurals (*e1–3*) are as in *Caproberyx* and living holocentrids. The stegural is fused with the underlying centrum (*pu1 + u1 + u2 + st*) anteriorly. The second uroneural (*d2*) is free and lies below and behind the first, not notched into the first as it is in living holocentrids. The second ural centrum is fused to the compound first pre-ural and ural centrum in AUB 108923 (standard length *c.* 75 mm.) although the line of fusion is clearly seen, but in AUB 108929, a much smaller specimen (standard length *c.* 35 mm.) the centrum appears free. As in living holocentrids, there are only five hypurals (*h1–5*), the small sixth hypural present in *Caproberyx* having been lost. As in *Myripristis*, the foremost caudal rays are inserted on the first epural above and the haemal spine of the third pre-ural centrum below, and there are four spines and one segmented ray in front of both the upper and lower principal rays.

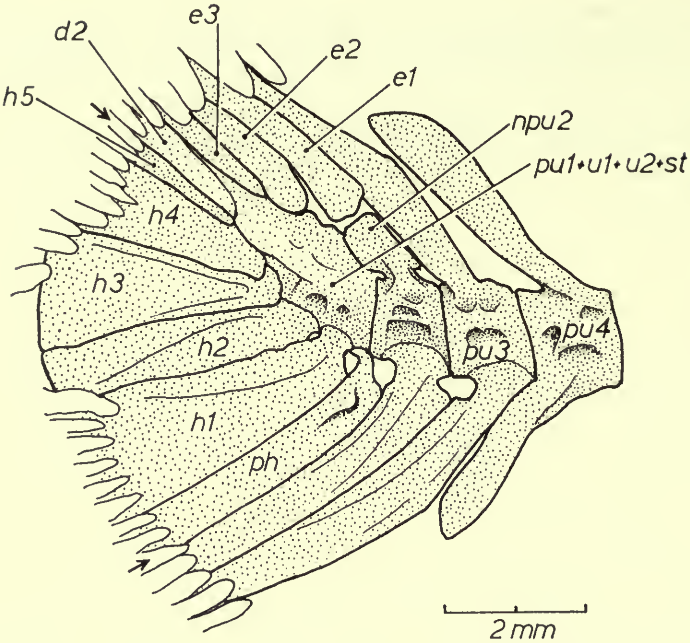


FIG. 22. *Stichocentrus liratus* Patterson. Caudal skeleton of AUB 108923, standard length *c.* 75 mm., Middle Cenomanian, Hajula, Lebanon. For explanation of lettering see p. 102. Arrows mark the outermost (unbranched) principal fin-rays.

As in the skull and fins, *Stichocentrus* is more advanced towards the living holocentrids than *Caproberyx* in the expanded neural and haemal spines of the fourth pre-ural centrum, the five hypurals and the partial fusion of the stegural and second ural centrum with the preceding centrum.

The remaining Cretaceous holocentrids are *Trachichthyoides ornatus* Smith Woodward (1902), known only by an isolated head from the English Chalk, and *Kansius sternbergi* Hussakof (1929) known by the two syntypes from the Niobrara Formation, Gove Co., Kansas. Nothing is known of the caudal anatomy of these forms.

Order LAMPRIDIFORMES

Suborder LAMPRIDOIDEI Berg (1940 : 463)

This suborder is used to contain both the Lampridoidei (*Lampris* only) and the Veliferoidei (*Velifer, etc.*) of Berg (Bonde 1966).

? Family **VELIFERIDAE** Bleeker (1860)

Genus ***BATHYSOMA*** Davis (1890 : 424)

The type and only species is *B. lutkeni* Davis from the Danian stage of southern Sweden. The caudal skeleton is partially preserved in two specimens in the British Museum (Natural History). P.9947 (Fig. 23A) shows that the upper hypurals are fused into a triangular plate and that this plate is fused basally with the second ural centrum (*u2* + *uh*). Above the second pre-ural centrum (*pu2*) and the fused first pre-ural and ural centra (*pu1* + *u1*) there are two elongate bones: the second of these (*e*) is certainly an epural but it is impossible to be certain whether the first is an epural or the neural arch and spine of the second pre-ural centrum. Above the upper hypural plate there is a third slender bone of uncertain nature. P.9948

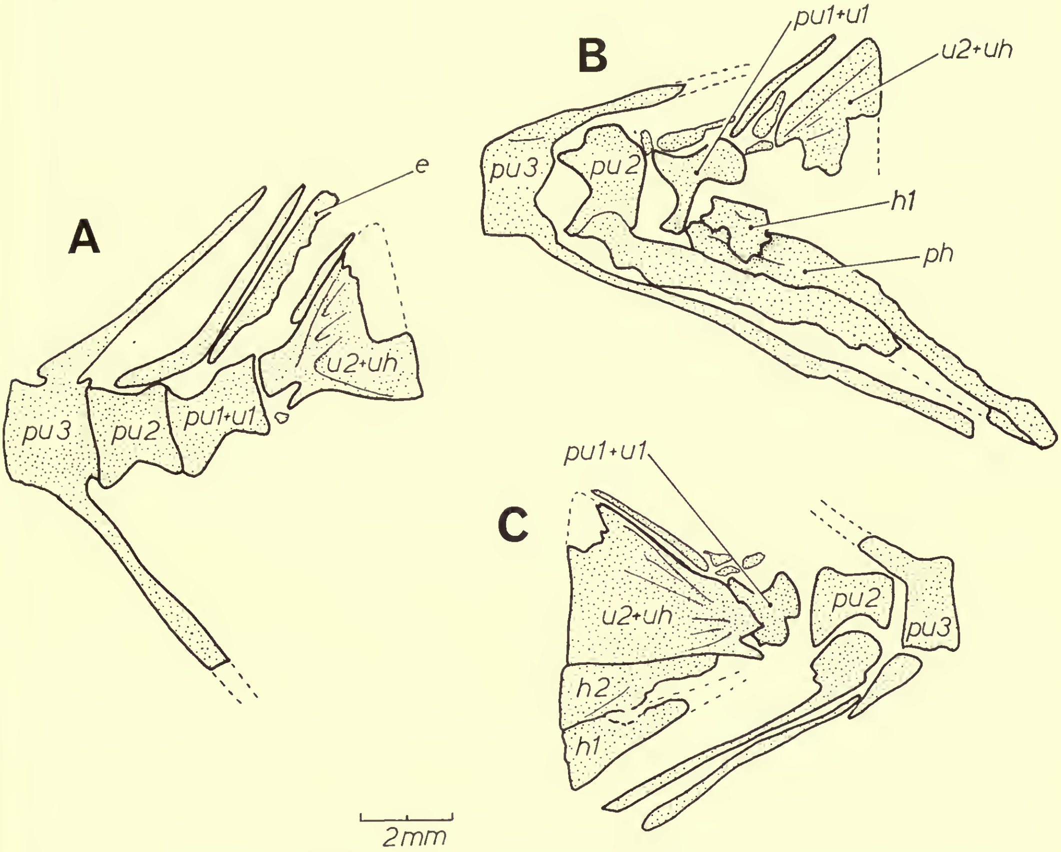


FIG. 23. *Bathysoma lutkeni* Davis. Caudal skeleton of **A**, P.9947, standard length *c.* 95 mm.; **B**, **C**, P.9948 (part and counterpart), standard length 78 mm. Both from Danian, Limhamn, southern Sweden. *u2* + *uh*, second ural centrum fused with one or more upper hypurals; for explanation of other lettering see p. 102.

(in counterpart, part and counterpart shown in Fig. 23B, C) shows the second pre-ural centrum (*pu2*) with an autogenous haemal arch and no sign of a neural spine, the fused first pre-ural and ural centra (*pu1* + *u1*) bearing the parhypural (*ph*) and the first hypural (*h1*) ,the distal part of the second hypural (*h2*), and the upper hypural plate with a fragment of the second ural centrum fused to it (*u2* + *uh*). As in P.9947, there is a slender bone lying above the upper hypural plate. The bones above the first and second pre-ural centra are shattered and displaced. Although these two specimens are far from complete, they show that in *Bathysoma* the haemal arch of the second pre-ural centrum was autogenous, the first pre-ural and ural centra were fused, the parhypural and the first and second hypurals were separate and autogenous, there was at least one epural, and the upper hypurals were fused with each other and with the second ural centrum. On the available material it is difficult to interpret the upper hypural plate and the slender bone above it, which may be an epural, a stegural or a free hypural. In the upper hypural plate at least three hypurals can be recognized in transparency under xylene, presumably hypurals 3–5, but the uppermost part of the plate is of a different texture, suggesting that the stegural may also be fused into the structure, a most unusual condition which can only be confirmed on more complete material.

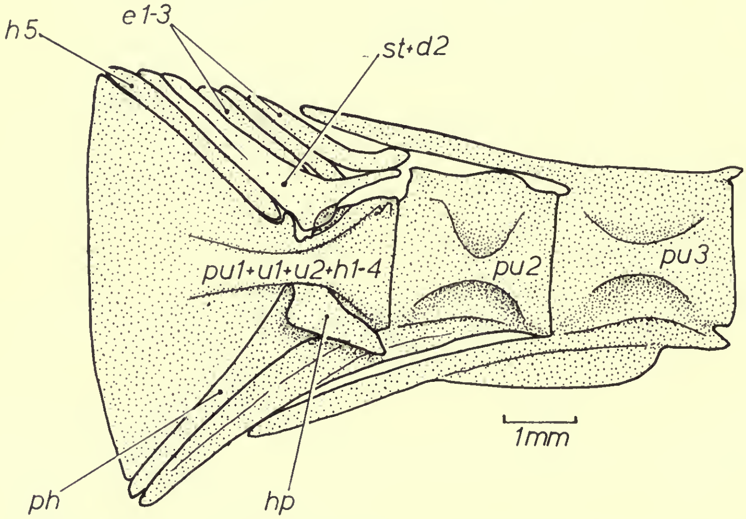


FIG. 24. *Mene maculata* (Bloch & Schneider). Caudal skeleton of a dried skeleton, 1866.6.8.59, standard length 95 mm., Taiwan. *hp*, hypurapophysis; for explanation of other lettering see p. 102.

The caudal skeleton of *Bathysoma* is very different from that of *Mene*, the only genus of the Menidae, in which *Bathysoma* was previously placed (Patterson 1964: 423). In the living *Mene maculata* (Fig. 24) the first pre-ural centrum, both the ural centra, and all but the uppermost hypural are fused into a symmetrical, fan-shaped plate (*pu1* + *u1* + *u2* + *h1–4*). The parhypural (*ph*) has a very large hypurapophysis (*hp*) and lies free below this plate. The uppermost hypural (*h5*) is also free, articulating with a hook on the upper edge of the hypural plate. There are three normal epurals (*e1–3*) and the neural arch of the second pre-ural centrum (*pu2*) is reduced to a very low crest. The stegural (*st* + *d2*) is autogenous, articulating with the underlying compound centrum by a large and clearly mobile joint. The distal part of the shaft of the stegural is grooved longitudinally in *M. maculata*; in the Middle Eocene species *M. rhombeus* (Volta) and *M. oblongus* (Agassiz), in which the caudal skeleton is otherwise identical with that of the living species, there is a free second uroneural, and the groove on the shaft of the stegural in *M. maculata* clearly marks the line of fusion between the first and second uroneurals. *Mene* has seventeen principal caudal rays with fifteen branched, the outermost two or three rays unsegmented and the inner ones only sparsely segmented, preceded by five unsegmented but divided (in the median plane) rays above and four below. The bases of the caudal rays are deeply cleft, covering much of the hypural plate. The caudal skeleton of *Mene* can be derived from the basal perciform type (p. 87) by fusion of the first four hypurals with each other and with the supporting centra, and the caudal fin has the perciform number of rays. The caudal skeleton of *Bathysoma* is of a much more primitive type, differing from that of Beryciformes mainly in the fusion of the upper hypurals with the second ural centrum. A caudal skeleton of this type occurs in the Lampridiformes *Velifer* (Gosline 1961; fig. 3D), *Palaeocentrotus* (Kühne 1941, fig. 2; Bonde 1966) and *Lampris*, and the known skeletal features of *Bathysoma* (Patterson 1964, fig. 90) agree as well with *Palaeocentrotus* and *Velifer* (Regan 1907; Smith 1951) as they do with *Mene*. The holotype of *Bathysoma lutkeni*, in Copenhagen, shows that the supraoccipital crest is attached to the skull roof only at the posterior end, with a gap between it and the frontal crest (Bonde, personal commn): an exactly similar supraoccipital crest occurs in Bonde's (1966) ? veliferid from the Lower Eocene [Mo-clay], while in *Palaeocentrotus* there is a large foramen between the supraoccipital and frontal crests (Kühne 1941, fig. 3). Provisionally *Bathysoma* may be placed in the Veliferidae but, like Bonde's Eocene form, it may well prove to be closer to *Palaeocentrotus*.

Order SALMONIFORMES (Greenwood *et al.* 1966)

Suborder MYCTOPHOIDEI

The most generalized of living myctophoids is *Aulopus* (Aulopodidae, Regan 1911*a* : 121). The caudal skeleton of *Aulopus* is briefly discussed by Gosline (1961 : 10), who notes that this genus is one of the few living teleosts retaining large caudal scutes in front of the caudal lobes. The caudal skeletons of more advanced myctophoids have been figured by Hollister (*Synodus*, *Trachinocephalus*, 1937*a*, figs 1–14), Gosline (*Chlorophthalmus*, 1961, fig. 2B), Rosen (*Myctophum*, 1964, fig. 23C) Greenwood *et al.* (*Neoscopelus*, 1966, fig. 3C) and Weitzman (*Parasudis* and *Saurida* 1967, figs 17, 18). In *Aulopus* the caudal skeleton is almost identical with that of the Cretaceous *Ctenothrissa* (Figs 4, 5), with a free second ural centrum, a stegural and a second uroneural, three epurals and six hypurals, of which the first and third are the largest. The only differences from *Ctenothrissa* are that the haemal arch of the third pre-ural centrum and the neural arch of the second pre-ural centrum are autogenous, the neural spine of the second pre-ural centrum is less expanded, more spine-like, and just over half as long as its predecessor, and the second ural centrum has a long posterior process. In all these characters, *Aulopus* appears to be more primitive than *Ctenothrissa*. In other living myctophoid families conditions are much as in *Aulopus*, but the caudal scutes are lost, the neural spine of the second pre-ural centrum ceases to be autogenous and becomes shorter and expanded, the first epural tending to move forwards above it, there is often fusion within the upper and lower hypurals, the sixth hypural and one epural may be lost (Synodontidae), and the second ural centrum and stegural may fuse with the compound first ural and pre-ural centrum. These trends are very like those seen within the Berycoidei (p. 68; cf. figs. 23C, D *in* Rosen 1964).

In the Upper Cretaceous myctophoids were abundant, the best known genera being *Sardinioides*, *Acrognathus*, *Cassandra* (= *Leptosomus*) and *Nematonotus*. *Nematonotus* appears to be the most primitive of these and will serve as an example. Figure 25 shows specimens of *Nematonotus bottae* (Pictet & Humbert), from the Cenomanian of Hakel, Lebanon, and *N. longispinus* (Davis), from the Cenomanian

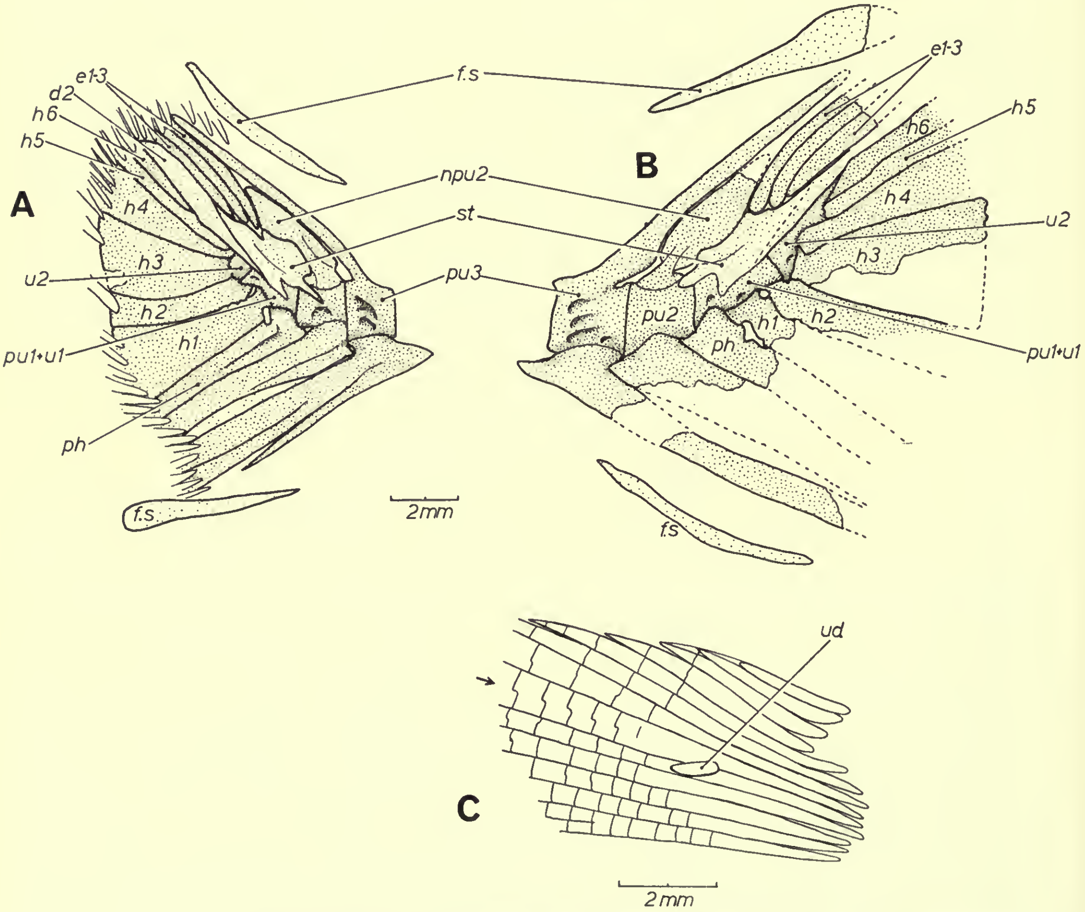


FIG. 25. The caudal skeleton in **A**, *Nematonotus bottae* Pictet & Humbert, 49563, standard length *c.* 90 mm., Middle Cenomanian, Hakel, Lebanon; **B**, *Nematonotus longispinus* (Davis), P.13882, standard length 114 mm., Middle Cenomanian, Hajula, Lebanon. In **C** are the bases of the upper caudal rays in P.48825, *N. longispinus*, standard length 97 mm., to show the urodermal, *ud*. For explanation of other lettering see p. 102. In **B** the second uroneural is missing, in **A** and **C** arrows mark the outermost (unbranched) principal fin-rays.

of Hajula, Lebanon. There are no significant differences between these two species in the caudal region. In the specimen of *N. bottae* illustrated, the haemal arches of the third and fourth pre-ural centra are fused and the haemal spine of the third pre-ural centrum is partially doubled. This is an individual abnormality. As in *Aulopus* there is a large caudal scute (*f. s*) above and below the caudal skeleton and the neural spine of the second pre-ural centrum (*npu2*) is autogenous, spine-like and just over half as long as its predecessor. The autogenous haemal spines on the second and third pre-ural centra, three epurals (*e1–3*), six hypurals (*h1–6*), long second ural centrum (*u2*, Fig. 25B) and second uroneural (*d2*) are as in *Aulopus*. The stegural (*st*) is forked proximally, with a process extending forwards on to the second pre-ural centrum. This process, absent in *Aulopus* and Ctenothrissiformes, is a primitive feature present in *Elops* and some clupavids (Patterson 1967*a*, fig. 11) which indicates the double origin of the first uroneural (Regan 1910 : 355; Patterson 1968 : 226). In *Nematonotus* there is a single urodermal (Fig. 25C), a structure absent from living myctophoids and Ctenothrissiformes but also present in the Cenomanian *Sardinioides attenuatus*. In *Nematonotus* the foremost procurrent caudal rays articulate with the neural and haemal spine of the third pre-ural centrum and the nineteen principal rays are preceded by four unsegmented and four segmented rays above, four unsegmented and two segmented rays below. In myctophoids the procurrent caudal rays are normally longitudinally divided, not spinous, but procurrent caudal spines appear in advanced members of the family Myctophidae (Fraser-Brunner 1949 : 1033).

III. DISCUSSION

(*a*) *The relationships of Ctenothrissiformes, Myctophoidei and Beryciformes.*

Monod (1967 : 118) has remarked that the structure of the caudal skeleton is rarely of value in discriminating between taxa at the generic level and below, but that it becomes increasingly valuable at the familial, subordinal and ordinal level. This observation is fully borne out by the forms described here, the only exception being the occurrence of two types of caudal skeleton in the ctenothrissiform family Aulolepididae, *Pateroperca* having the neural spine of the second pre-ural centrum fully developed, *Aulolepis* having it short and expanded, as it is in Ctenothrissidae. This suggests that *Aulolepis* and *Pateroperca* belong to different families, but *Pateroperca* is as yet so poorly known that no conclusion can be reached on this point until more specimens are discovered.

Among the Ctenothrissiformes, Myctophoidei and Beryciformes caudal anatomy is very similar. The basal type of caudal skeleton in these groups has the following features: the first pre-ural and ural centra fused, a free second ural centrum, three epurals, a stegural, a second uroneural and six hypurals (two lower and four upper). Caudal scutes above and below the caudal skeleton are present in *Aulopus*, most Cretaceous myctophoids (*Nematonotus*, *Acrognathus*, *Sardinioides*) and Ctenothrissiformes (*Aulolepis*, *Ctenothrissa*): they are absent in Beryciformes and higher groups. A single urodermal is present in *Nematonotus* and *Sardinioides attenuatus* among Cretaceous myctophoids. There is no urodermal in Ctenothrissiformes or Beryciformes. The main variations encountered in the caudal skeletons of myctophoids, ctenothrissiforms and beryciforms involve reductions in the number of caudal elements by fusion or suppression and the condition of the neural spine of the second pre-ural centrum, which may be fully developed (*Pateroperca*, Polymixioidei, *Pycnosteroides, Dinopteryx*), spine-like and about half as long as its predecessor (*Nematonotus, Aulopus, Aipichthys, Pharmacichthys*), short and expanded (*Ctenothrissa, Aulolepis*, many myctophoids) or reduced to a low crest (Berycoidei).

The basal teleostean caudal skeleton, seen in such genera as *Leptolepis, Allothrissops, Thrissops, Ichthyodectes, Hiodon, Elops, Salmo*, etc., contains two free ural centra, three epurals, two lower hypurals and five upper hypurals (there may be six or seven upper hypurals in *Leptolepis*; Patterson 1968 : 220; there are only four in salmonids; Norden 1961 : 738), up to seven uroneurals (Patterson 1968) which extend forwards to the fourth pre-ural centrum in *Thrissops* and *Ichthyodectes*, to the third in *Leptolepis* and *Allothrissops* and to the second pre-ural centrum in *Hiodon, Elops, Salmo*, etc., and one or two urodermals (Patterson 1968 : 230). The condition of the neural arches and spines in the caudal region is often complicated by doubling of the segmental structures, usually as individual variations, but in *Leptolepis, Allothrissops, Elops* and some salmonids there is normally a neural arch and spine on the first pre-ural centrum, and in *Leptolepis, Hiodon*, osteoglossoids (Greenwood 1967) and *Alepocephalus* (Patterson 1968, fig. 12) there may be a more or less well developed arch and spine on the first ural centrum. It is usually assumed (e.g. Gosline 1961 : 14; Patterson 1967*a* : 104) that the second pre-ural centrum primitively bears a complete neural spine, supporting epaxial fin-rays. But among the forms described here the most primitive (*Aulopus, Nematonotus*) have the neural spine of the second pre-ural centrum about half as long as that of the third, and this is also true of *Elops* (Nybelin 1963, figs. 1, 4), which in other respects seems to be the most primitive living teleost. This suggests that the short second pre-ural neural spine may be primitive for some teleost groups. There are three possible conditions of the second pre-ural neural spine. It may be fully developed, as in *Allothrissops* (Patterson 1967*a*, fig. 6), *Ichthyodectes* (Cavender 1966, fig. 1), *Tarpon* (Nybelin 1963, fig. 7), and many other primitive telosts, normally supporting epaxial fin-rays but in *Tarpon* ending just in front of the foremost epaxial fin-ray; it may be about half as long as its predecessor, as in *Elops*, "*Clupavus*" (Patterson 1967*a*, fig. 11), *Nematonotus* and *Aulopus*; or it may be represented only by a low crest, as in Berycoidei and generalized percoids (p. 87). Intermediates between the second and third of these conditions occur in *Aulolepis, Ctenothrissa* and many myctophoids. Intermediates between the first two conditions seem to occur only in primitive protacanthopterygian groups (salmonids, as in the specimen of *Cristivomer* illustrated by Vladykov 1954, fig. 2; characinids, as in the specimen of *Brycon* illustrated by Weitzman 1962, fig. 15) in which the pre-ural neural spines are very variable and both conditions may occur in a single species. The third condition, the spine reduced to a low crest, is undoubtedly advanced and may be left out of consideration here. In the ancestors of the teleosts, the pholidophorids, the neural spines of the last three pre-ural vertebrae decrease in size progressively so that all three end on approximately the same oblique plane: the first pre-ural neural spine is very short, the second is both shorter and more slender than the third (Patterson 1968, figs. 1–4). In pholidophorids these neural spines do not reach the dorsal edge of the trunk and do not support fulcra or fin-rays. This condition of the pre-ural neural spines seems to be primitive for the teleosts as a whole and it persists in the Lower Jurassic *Leptolepis coryphaenoides* and *L. normandica* (Nybelin 1963, figs. 9, 10) and the Upper Jurassic *L. dubia* (Nybelin 1963, fig. 8; Patterson 1968, fig. 10). In the Upper Jurassic two of the three modern types of second pre-ural neural spine were already in existence. In *Allothrissops* and *Thrissops* (Nybelin 1963, figs. 11, 12; Patterson 1967*a*, fig. 6) both the second and third preural neural spines have elongated so that they reach the dorsal edge of the trunk, ending just in front of the foremost procurrent fin-rays: this is essentially the condition in living *Tarpon*. In the Upper Jurassic *Elops*-like fish illustrated by Nybelin (1963, fig. 6) the second pre-ural neural spine remains short but the third and fourth pre-ural neural spines are elongated, reaching the dorsal edge of the trunk and supporting the foremost procurrent fin-rays. This is essentially the condition in living *Elops*. There is no *a priori* reason to regard either of these two conditions as more primitive, both are a response to a new need, the necessity to support the epaxial procurrent rays as they extend forwards to increase the dorso-ventral symmetry of the tail. However, we know that the *Elops* type, with a short second pre-ural neural spine, has persisted unchanged in elopids since the Upper Jurassic and that this type of second pre-ural neural spine is primitive for the teleosts as a whole, and there is no reason for regarding the short neural spine of *Elops* and its Jurassic relative as a secondary regression from a long neural spine of *Tarpon* type. I conclude, therefore, that when one finds a second pre-ural neural spine resembling that of *Elops* in a generalized teleost one should regard it as a primitive feature unless there is good evidence to the contrary. In support of this interpretation is the occurrence of a second pre-ural neural spine of this type only in teleosts in which the caudal skeleton retains such primitive features as a free second ural centrum and nineteen principal caudal rays. A generalized teleost having an elongate second pre-ural neural spine is to be regarded as having developed this from a short spine of leptolepid or elopid type: this development can apparently take place spontaneously (see *Aipichthys*, Fig. 11).

From the basal type of teleostean caudal skeleton, the most primitive members of the myctophoid-ctenothrissiform-beryciform assemblage (such as *Nematonotus*) differ in the loss of one hypural, the seventh, whether by suppression or by fusion with the sixth is as yet unknown, have reduced the number of uroneurals to two, principally by loss of the small posterior uroneurals (ural neural arches 6–8), since the forked first uroneural of *Nematonotus* (Fig. 25) is clearly homologous with that of *Elops*, representing the second and third ural neural arches, while the second uroneural is probably homologous with the second uroneural of *Elops*, representing the fourth and fifth ural neural arches (Patterson 1968 : 226), the first pre-ural and ural centra have fused, and the first uroneural has fused with the first ural and pre-ural neural arches to produce a stegural, a development which took place very early in the protacanthopterygian lineage (salmonids, " *Clupavus* ", etc.). These changes raise the question of the origin of the myctophoids and ctenothrissiforms. Greenwood *et al.* (1966 : 371) wrote of the ctenothrissiforms " we link them with some early group of myctophoid-like salmoniform fishes in which the supramaxillae were not reduced, the premaxilla had not excluded the maxilla from the gape, and in which the adipose fin had disappeared." By extension, the ancestor of the myctophoids would be such a fish with an adipose fin. On the other hand, Gosline (1961 : 35; also Gosline, Marshall & Mead 1966 : 5) points out that the large caudal scutes of *Aulopus* make it impossible to derive the myctophoids from any living teleost except the elopoids. Weitzman (1967 : 532) discusses this point and notes that caudal scutes are present in *Argentina*, but the structures he describes in the salmonoid *Plecoglossus* and the galaxioid *Retropinna* do not seem to resemble caudal scutes. The absence in all known salmonoids of large caudal scutes and of a forked first uroneural of the type found in *Elops* and *Nematonotus*, together with the absence of recognizable salmonoids from pre-Tertiary rocks, make it difficult to envisage any direct relationship between salmonoids and myctophoids (Greenwood *et al.* 1966, fig. 1). A short second pre-ural neural spine resembling those of *Aulopus* and *Nematonotus* occurs in some salmonoids (*Coregonus*, which also has a urodermal), but the last few neural arches and spines and the epurals are apparently very variable, and no clear pattern emerges from Norden's (1961 : 738) analysis. In *Argentina* caudal scutes are present (though they are reduced) and the first pre-ural and ural centra are fused (Gosline 1960, fig. 10), as they must have been in the common ancestor of Myctophoidei and Ctenothrissiformes, but the neural spine of the second pre-ural centrum is elongate and supports procurrent fin-rays: in this character *Argentina* is advanced over the basal myctophoids and ctenothrissiforms. In the Clupavidae, a family with a fossil record extending back to the Upper Jurassic, large caudal scutes are usually present in the tail, the skull seems primitive enough to have given rise to both myctophoids and Ctenothrissiformes, and the caudal skeleton may be strikingly like that of *Nematonotus* (Patterson 1967*a*, fig. 11). It is unlikely that the known clupavids were ancestral to the myctophoids and ctenothrissiforms because of their reduced dentition and clupeid-like jaws, with a high coronoid process on the dentary, but they suggest a possible source for this type of caudal skeleton.

Taking the caudal skeleton of *Nematonotus* as the primitive condition for the myctophoids and ctenothrissiforms, the myctophoids are characterized by shortening and broadening the neural spine of the second pre-ural centrum, and in more advanced forms by fusion of the hypurals with each other and with the supporting centra. Within the ctenothrissiforms two distinct types of caudal skeleton occur: in *Ctenothrissa* and *Aulolepis* the neural spine of the second pre-ural centrum is expanded, as in myctophoids, tending towards the condition in Berycoidei and Percoidei; in *Pateroperca* the second pre-ural neural spine is fully developed, as it is in Polymixioidei. In *Aulolepis* and some species of *Ctenothrissa* there are procurrent spines in front of the caudal fin: this is specific evidence of evolution towards the Berycoidei and like the reduction of the second pre-ural neural spine in these fishes it distinguishes them from the Polymixioidei and Dinopterygoidei, in which procurrent caudal spines occur only in advanced forms.

Within the Beryciformes, the structure of the caudal skeleton gives some support to the division of the order into three suborders. In Polymixioidei there are always six hypurals and the neural spine of the second pre-ural centrum is fully developed. In Berycoidei the second pre-ural spine is reduced to a low crest (except in one individual of *Monocentris*, Fig. 14), the procurrent rays are spinous, and there are trends towards loss of the sixth hypural and fusion of the stegural and second ural centrum with the preceding centrum. In the Dinopterygoidei, already known to be a heterogeneous group, the neural spine of the second pre-ural centrum retains the primitive short condition (*Aipichthys*, *Pharmacichthys*) or is fully developed (*Dinopteryx*, *Pycnosteroides*) and there are trends towards loss of the sixth hypural. The polymixioid caudal skeleton (also found in *Dinopteryx* and *Pycnosteroides*) resembles that of the ctenothrissiform *Pateroperca*, differing only in having no caudal scutes and in having one less principal ray. The caudal skeleton of Berycoidei resembles those of *Aulolepis* and *Ctenothrissa*, differing only in having lost the caudal scutes and further reduced the second pre-ural neural spine. *Aipichthys* and *Pharmacichthys* seem to have the most primitive caudal skeletons known in Beryciformes, with nineteen principal rays, the primitive short second pre-ural spine, and, at least in some specimens of *Aipichthys*, six autogenous and separate hypurals and a free second ural centrum. Although both *Aipichthys* and *Pharmacichthys* are too specialized in other characters to have given rise to Beryciformes, their caudal skeleton could give rise to both the polymixioid condition (by elongation of the second pre-ural neural spine, which occurs spontaneously in some individuals of *Aipichthys*, Fig. 11C) and the berycoid condition (by shortening of the second pre-ural neural spine).

(*b*) *The origin of Perciformes.*

Gosline (1961*a*) discussed the caudal skeleton of Perciformes and found that the most generalized type contains fifteen branched principal rays, no neural spine on the second pre-ural centrum, three epurals, two free uroneurals, no free ural centra, five autogenous hypurals, and the haemal arches of the second and third pre-ural centra autogenous (see also Monod 1967, fig. 3). Gosline mentioned that this type of caudal skeleton occurs in *Kuhlia* (Kuhliidae), *Chaetodon* (Chaetodontidae), *Polydactylus* (Polynemoidei) and juvenile *Sphyraena* (Sphyraenoidei). Monod (1967) refers to this type of caudal skeleton as " sciaeno-sparidien banal " and states that it occurs in many Perciformes, mentioning *Sciaena* (Sciaenidae), *Pagrus*, *Sparus* (Sparidae) and *Gaterin* (Pomadasyidae). I find that this generalized type of caudal skeleton also occurs in *Centropomus* (Centropomidae), *Lateolabrax*, *Polyprion*, *Dicentrarchus*, *Morone*, *Acanthistius* (Percichthyidae, *sensu* Gosline 1966), *Branchiostegus* (Branchiostegidae), *Pomatomus* (Pomatomidae), *Brama* (Bramidae), *Arripis* (Arripidae), *Lutjanus* (Lutjanidae), *Nemipterus*, *Scolopsis* (Nemipteridae), *Lobotes* (Lobotidae), *Xenocys*, *Xenistius*, *Xenichthys* (Pomadasyidae), *Lethrinus*, *Sphaerodon* (Lethrinidae), *Monodactylus* (Monodactylidae), *Kyphosus*, *Medialuna* (Kyphosidae), *Ephippus*, *Drepane*, *Platax* (Ephippidae), *Chelmo*, *Heniochus*, *Pomacanthus* (Chaetontidae), *Histiopterus* (Pentacerotidae), *Cirrhitus* (Cirrhitidae) and *Schedophilus* (Stromateoidei). Many other groups, among them the Serranidae (*sensu* Gosline 1966), Cichlidae, Percidae, Acanthuroidei, etc. differ from this basal type only in the loss or incorporation in the stegural of the second uroneural. The occurrence of an apparently identical type of caudal skeleton in such a wide range of perciform groups, including forms with lunate, forked, emarginate and rounded caudal fins in habitats ranging from pelagic to lacustrine, suggests that caudal anatomy is unlikely to contribute much to the unravelling of lineages among generalized Perciformes.

A caudal skeleton very similar to the basal perciform type occurs in some advanced Berycoidei (living Holocentridae and Diretmidae differ only in having the stegural fused with the underlying centrum (Fig. 20), Berycidae have the stegural fused with the centrum and also retain the sixth hypural (Regan 1911, fig. 1)) but here the hypurals support nineteen principal rays. In Myctophoidei a slightly different sequence of fusion is followed in which the second ural centrum partially retains its individuality. So far as I know, the basal perciform caudal skeleton is not precisely duplicated elsewhere.

The differences between the caudal skeleton and fin of basal Perciformes and those of generalized Beryciformes (*Polymixia*, *Aipichthys*, *Pycnosteroides*, *Monocentris*) are:

(i) Reduction of the neural spine of the second pre-ural centrum. This has already taken place in all Berycoidei.

(ii) Fusion of the second ural centrum with the preceding two centra. This has taken place in most living Berycoidei and occurs in some individuals of *Aipichthys*.

(iii) Loss of the sixth hypural (the development of the caudal skeleton in *Mugil* and *Sphyraena* (Hollister 1937) suggests that Perciformes have lost the sixth hypural, not incorporated it in the fifth). This has already occurred in some individuals of *Aipichthys* and *Pycnosteroides*, and takes place during the evolution of the Berycoidei (Holocentridae, *Diretmus*).

(iv) Reduction of the number of principal caudal rays from nineteen (Berycoidei, *Aipichthys* and *Pharmacichthys*) or eighteen (Polymixioidei, *Dinopteryx* and *Pycnosteroides*) to seventeen.

(v) In all living Beryciformes, the foremost procurrent rays in each caudal lobe are true spines, but in Perciformes they are usually (? always) unsegmented lepidotrichia, with the right and left halves separate, and this is true of the earliest Perciformes (*Prolates*). In this character Perciformes are more primitive than living Beryciformes. Among Cretaceous Beryciformes, all Berycoidei, like their living relatives, have spines in front of the caudal fin; in Polymixioidei procurrent spines occur only in *Homonotichthys* and *Pycnosterinx dubius*, already known to be evolving towards the living *Polymixia* (Patterson 1964 : 301, 380), and in Dinopterygoidei they occur only in *Dinopteryx*. It is striking to find that spinous procurrent caudal rays occur only in those Cretaceous genera (except *Dinopteryx*) already known to be closely related to living Beryciformes.

The first of these five differences, the condition of the neural spine of the second pre-ural centrum, is the most interesting. As discussed above (p. 84) the primitive condition of this structure in teleosts seems to be as in *Elops*, *Aulopus* and *Nematonotus*, where the spine is slender and about half as long as its predecessor. This type of spine may elongate so that it supports procurrent fin-rays, as in Polymixioidei and many primitive telosts, or it may become reduced to the percoid condition (Fig. 28). But apart from these two simple alternatives there are other possibilities which complicate the issue. First, the fully developed spine might become detached as an epural, producing the percoid condition direct. Secondly, from a low neural crest of percoid type an apparent full neural spine might develop secondarily by fusion with the first epural. Thirdly, an apparent neural spine on the second pre-ural centrum might be produced by fusion between the second and third pre-ural centra. The last of these possibilities can normally be recognized by the partial or complete doubling of the neural or haemal spine on the compound centrum, as in *Pleuronectes* (Barrington 1937, fig. 1) and the specimen of *Saurida* illustrated by Weitzman (1967, fig. 18). The abnormal specimen of *Monocentris* illustrated in Fig. 14 is evidently a special case of this type of fusion, where the neural and haemal spines of the third pre-ural centrum are normally double and the posterior half of the neural spine has become attached to the succeeding centrum. This type of fusion does not seem of general significance in the present discussion.

Fusion of an epural with the neural crest of the second pre-ural centrum to produce a secondary neural spine (Fig. 28E) is a common occurrence in acanthopterygians: this process appears to account for the complete neural spine on the second pre-ural centrum in such groups as the Nandidae (but not *Pristolepis*; Gosline 1968, fig. 2*b*) among Percoidei, the Channiformes, Anabantoidei, *Luciocephalus*, some scombroids, pleuronectoid and soleoid pleuronectiforms, tetraodontiforms, etc. (Monod 1967; Liem 1963, 1967; Gosline 1968). In *Psettodes*, the most primitive living pleuronectiform, the caudal skeleton (Monod 1967, fig. 13) is of basal perciform type, with five autogenous hypurals and two uroneurals, but there is only one free epural and there appears to be a neural spine on the second pre-ural centrum. Monod identifies this spine as the first epural, for the element is partially or completely autogenous and the suture at the base lies not between the arch and the centrum but between the arch and the spine. *Psettodes* demonstrates clearly that the neural spine of the second pre-ural centrum in Pleuronectoidei and Soleoidei is an epural which has secondarily regained contact with and fused with a neural arch. That this has also occurred in scombroids such as *Neothunnus* can be seen by comparing figs. 15 and 16 of Monod (1967). A further peculiarity of the caudal skeleton of pleuronectoids and soleoids is that the parhypural tapers proximally and fails to make contact with the centrum (Monod 1967 : 117). The effect of this is to give dorso-ventral symmetry to the caudal skeleton, the free parhypural opposing the single epural just as the neural and haemal spines of the second pre-ural centrum oppose one another. A free parhypural, tapering proximally, also occurs in acanthopterygians such as the Channiformes (Monod 1967 : 117; Gosline 1968, fig. 2*a*), most Anabantoidei (Liem 1963 : 32), *Luciocephalus* (Liem 1967 : 114) and balistoids (Whitehouse 1910, pl. 50, fig. 33; Monod 1967 : 117), all forms with a neural spine on the second pre-ural centrum. Since none of these fishes has more than two epurals, all these groups appear to be cases of secondary fusion between the first epural and the second pre-ural neural arch in order to increase the dorso-ventral symmetry of the caudal skeleton. A complete neural spine on the second pre-ural centrum also occurs occasionally in basal percoids: Fig. 26 shows such a structure in a large specimen of *Siniperca* (Percichthyidae). In this individual there is a perfectly formed neural arch and spine (*npu2*) fully fused to the second pre-ural centrum, and there are only two epurals (*e1, 2*) compared with the three of normal *Siniperca*, most percichthyids and serranids. This specimen is best regarded as an abnormality foreshadowing the fusion of the first epural with the second pre-ural neural arch in nandids, pleuronectiforms, etc.

It is thus well established that in many perciform groups and perciform derivatives the first epural can fuse with the second pre-ural neural arch. This raises the question of the homology of the perciform first epural: does the frequent fusion of this bone with the second pre-ural centrum indicate that these two structures were

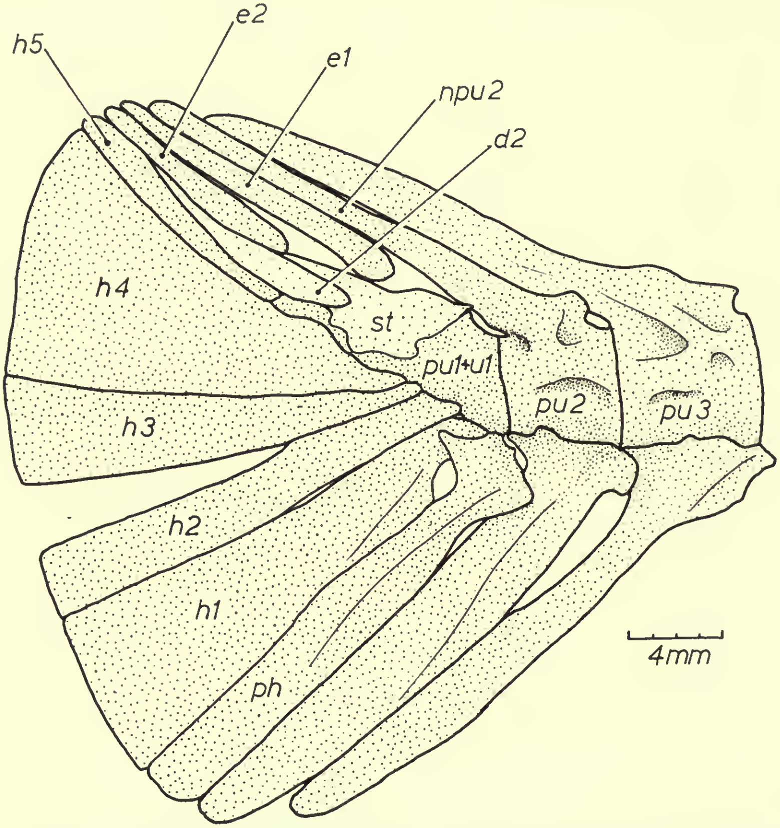


FIG. 26. *Siniperca chuatsi* (Basilewsky). The caudal skeleton of a dried skeleton showing a complete neural spine on the second pre-ural centrum, 1888.3.23.3, standard length 340 mm., Kiu Kiang, China. For explanation of lettering see p. 102.

originally part of the same segment? If so, the perciform first epural may have appeared by detachment of a fully developed neural spine in a caudal skeleton of polymixiid type. Rosen (1964 : 244) suggested that this took place in the evolution of the exocoetoids: that the ancestral exocoetoid had only two epurals and a fully developed neural spine on the second pre-ural centrum which became detached as the foremost of the three epurals in such a fish as *Dermogenys*. If this neural spine became detached in a fish which still retained the original three epurals one would expect there to be four epurals. Such a condition occurs very occasionally in

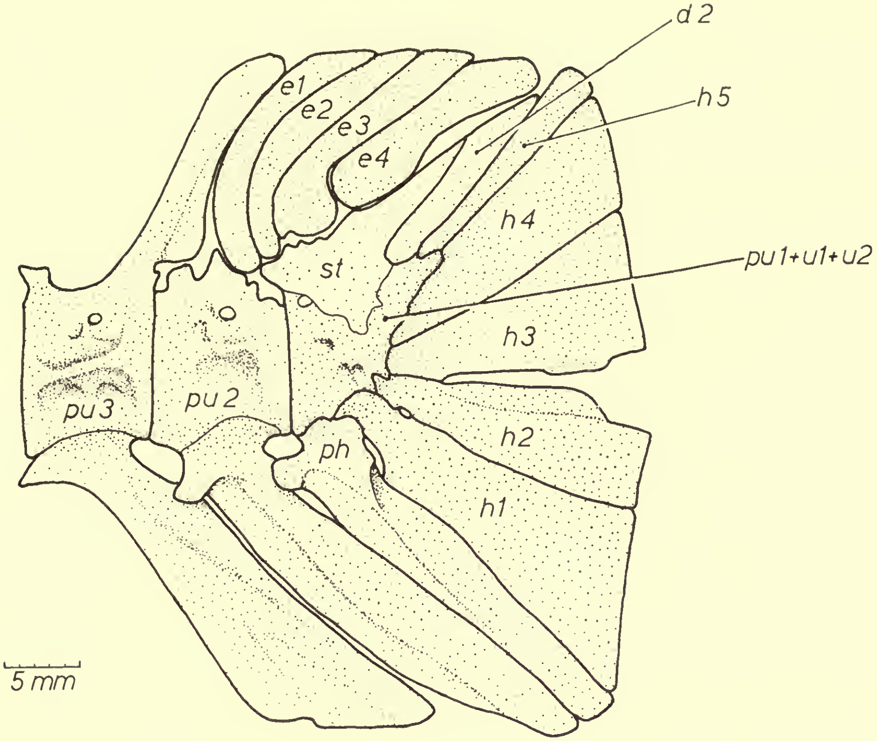


Fig. 27. *Pentaceropsis recurvirostris* (Richardson). Caudal skeleton of a dried skeleton showing four epurals, 1869.2.24.24, standard length 405 mm., Tasmania. For explanation of lettering see p. 102.

the generalized percoid caudal skeleton, as in the individual of *Pentaceropsis* (Pentacerotidae) shown in Fig. 27.

The epurals of teleosts are the remnants of a more numerous set of bones in primitive actinopterygians which are serial homologues of the supraneurals above the anterior vertebrae, and like these bones they were primitively metameric (Patterson 1968 : 221), but the metameric arrangement of the epurals has been lost in living chondrosteans. In the most primitive teleosts, such as the Jurassic *Leptolepis* and *Allothrissops* (Patterson 1967*a*, figs. 3, 6), the three epurals still show an apparent metamery, suggesting that they represent the neural spines of the first pre-ural neural arch and two ural neural arches: this seems to be supported by conditions in osteoglossoid fishes, where there are often fully-developed neural spines on both the first pre-ural and the first ural centra, and where there is never more than one epural (Greenwood 1967). But in higher teleosts, as in living chondrosteans, a metameric arrangement of the epurals is no longer recognizable. At the percoid level, for example, one can find fishes with all the epurals behind the neural crest on the second pre-ural centrum (Gosline 1961*a*, fig. 1, *Kuhlia*; 1968, fig. 5*c*, *Bathymaster*), or with one epural above the crest (Gosline 1961*a*, fig. 2, *Parupeneus*; Hollister 1937, figs. 12–14, *Sphyraena*) or with two above it (Hollister 1937, fig. 8, *Mugil*). Further, in groups such as the Berycoidei and Percoidei there is good evidence that in primitive forms the first epural lies behind the neural crest of the second pre-ural centrum, moving forwards above it in more advanced forms (in berycoids cf. Figs. 17, 21 with Figs. 13, 20). Since there is no evidence that strict metamery of the epurals is maintained in acanthopterygians there is no reason to believe that the perciform first epural is the detached neural spine of the second pre-ural centrum. The individual of *Pentaceropsis* shown in Fig. 27 is best interpreted merely as exhibiting a supernumary epural: such a condition is already known to occur in the salmonid *Oncorhynchus*, where Vladykov found four epurals in three out of 1,020 specimens (1962, table 8).

The conclusions drawn from this discussion of the second pre-ural neural arch and spine are that the low neural crest in basal percoids is to be regarded as having evolved by reduction of the primitive short neural spine, and that the ancestors of the perciforms are to be found among fishes having a low crest or short neural spine on the second pre-ural centrum, not among those with a full neural spine. Where there is a full neural spine on the second pre-ural centrum in Perciformes and perciform derivatives, it is to be regarded as having arisen by fusion of an epural with a low neural crest. These conclusions are illustrated in Fig. 28.

With this background on the perciform caudal skeleton, we can now consider the evidence of caudal structure in the various beryciform-perciform lineages that have been suggested (Patterson 1964). These were, in decreasing order of confidence,

Polymixiidae (*Omosoma—Berycopsis* lineage) ⟶ Scorpididae, Monodactylidae and Kyphosidae
Aipichthyidae ⟶ Carangidae
Pharmacichthyidae ⟶ Acanthuroidei
Sphenocephalidae ⟶ basal Percoidei (Serranidae, etc.)
Pycnosteroididae ⟶ Chaetodontidae
Dinopterygidae ⟶ Centrarchidae

Detailed study of the caudal skeleton cannot be said to give support to these lineages. Of the various perciform groups mentioned, the scorpidids, monodactylids, kyphosids, basal percoids (Centropomidae, Percichthyidae), Chaetodontidae and Centrarchidae have the generalized percoid type of caudal skeleton, differing from those of Beryciformes in the characters listed on p. 88. The acanthuroids are more advanced only in having lost the second uroneural, while the carangids have enlarged the first epural and show fusion between the first and second hypural and between the third and fourth hypurals. Among the beryciform groups, the polymixiids, sphenocephalids, pycnosteroidids and dinopterygids all have a complete neural spine on the second pre-ural centrum: for reasons given in the discussion above, it is unlikely that a percoid caudal skeleton can be derived directly from this condition. In *Sphenocephalus* there are only two epurals, suggesting the possibility of arriving at a percoid arrangement of three epurals and a low neural crest on the second pre-ural centrum by detachment of the neural spine on this centrum, but further study of *Sphenocephalus* has yielded strong evidence (to be discussed in a forthcoming paper by the author and D. E. Rosen) that far from being an ancestral percoid it is related to the percopsiforms. In the aipichthyids and pharmacichthyids

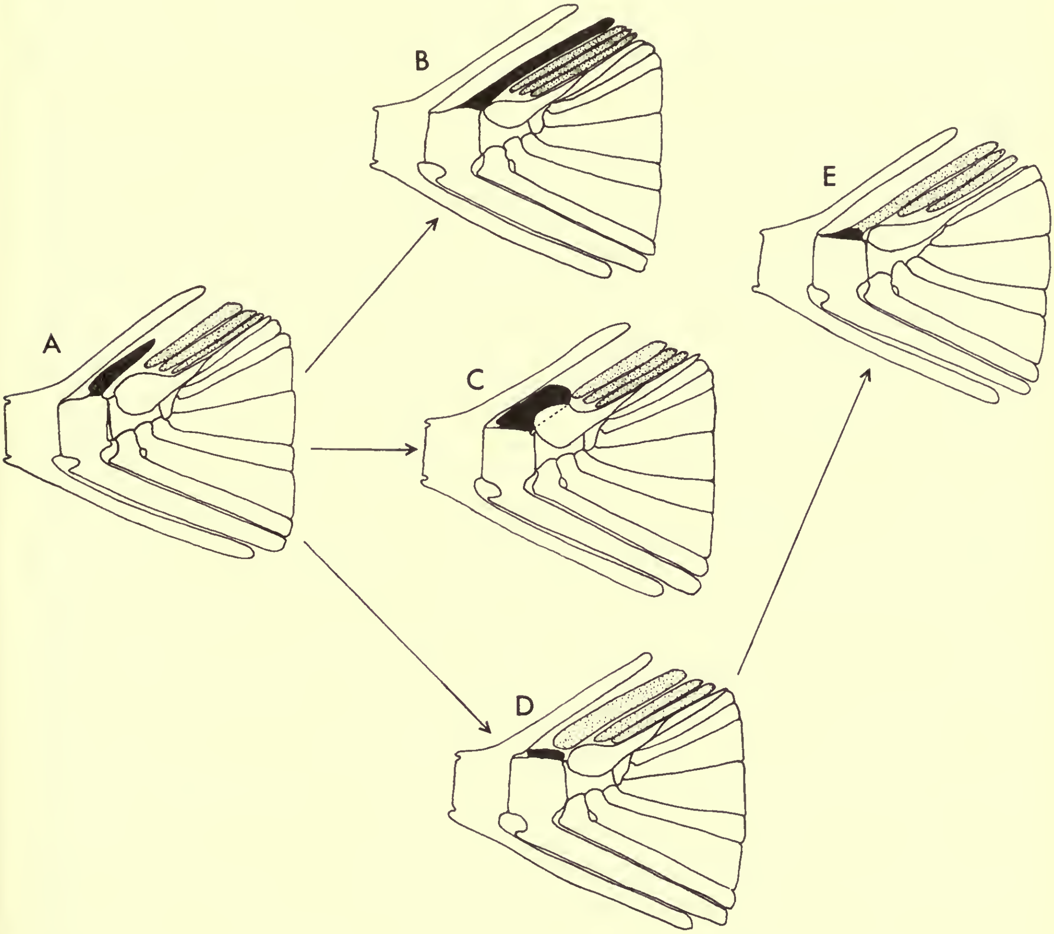


FIG. 28. Diagrams to show changes in the second pre-ural neural spine (black) in the evolution of the myctophoids, ctenothrissiforms and acanthopterygians. **A**, the primitive short neural spine, as in *Nematonotus*, *Aulopus*, *Aipichthys* and *Pharmacichthys*; **B**, elongation of the neural spine to support procurrent fin-rays, as in *Pateroperca*, Polymixiidae, *Dinopteryx* and *Pycnosteroides*; **C**, expansion of the neural spine into a plate, as in most myctophoids, *Ctenothrissa*, *Aulolepis* and some primitive Berycoidei; **D**, reduction to a low crest, with the first epural (stippled) moving forwards above it, as in most Berycoidei and Perciformes (a berycoid is illustrated); **E**, production of a secondary neural spine by fusion of the first epural in fishes with no free second ural centrum and five hypurals, as in Zeiformes (except Caproidae), Nandidae, Channiformes, Anabantoidei, Pleuronectiformes, etc.

the neural spine of the second pre-ural centrum is still short, as in the most primitive teleosts, and could give rise to the percoid condition by reduction. Further, in *Aipichthys* (Fig. 11) there is a tendency to reduce the number of hypurals to five and also to fuse the second ural centrum into the preceding centrum, as in percoids. There seems to be nothing in the caudal skeleton of *Aipichthys* to oppose the postulated link with the carangids. In *Pharmacichthys* the caudal skeleton is like that of *Aipichthys*, so far as it is known, and the fin-rays are deeply cleft basally, as in carangids: this character reduces the possibility of a relationship between *Pharmacichthys* and the acanthuroids and balistoids, in which the caudal fin-rays are unmodified.

Except for the *Aipichthys*-carangid lineage, the evidence of the caudal skeleton indicates that Gosline's (1966*a*) criticism of the polyphyletic scheme of perciform origins which I proposed are well founded. But the evidence on which Gosline based these criticisms, the structure of the supraoccipital crest, does not in fact oppose the various beryciform-perciform lineages. Gosline (1966*a* : 412) contrasted the type of supraoccipital crest seen in the polymixiids *Homonotichthys* and *Polymixia*, and in the carangids, priacanthids, etc., which extends forwards between the frontals, is knife-edged and buried in musculature, with the type of crest seen in *Antigonia*, acanthuroids, chaetodontids, etc., which is short, high and thickened anteriorly, extending " up and back over the nape as a sort of protective shell ". Gosline finds that these two types of supraoccipital crest are " structurally and functionally . . . far apart ", and writes " nor does it appear that one could be developed from the other except by going all the way back through some intermediate form with a relatively small, unspecialized occipital crest ". Gosline draws the conclusion that *Aipichthys* and *Sphenocephalus*, both with a short crest, thickened anteriorly, could not have given rise respectively to the carangids and serranids, which have a long, knife-edged crest. But the evolution of the Berycoidei shows (as clearly as such processes can be shown by the fossil record) that fishes with a short " *Aipichthys*-type " crest can give rise to fishes with a long " carangid-type " crest. The most primitive Berycoidei have an " *Aipichthys*-type " crest, moderately high and thickened anteriorly: this is true of both the trachichthyid lineage (*Lissoberyx*, Patterson 1967, fig. 2) and the holocentrid lineage (*Caproberyx*, Patterson 1964, fig. 67; 1967, fig. 10, *Stichocentrus*, Patterson 1967, fig. 8). From this basal type there are in berycoids two divergent trends in the evolution of the supraoccipital crest. In Holocentridae the frontals grow backwards, partially covering the parietals, eliminating the supratemporal fossa, and producing a low supraoccipital crest which secondarily comes to resemble the small supraoccipital crest of primitive teleosts. In Trachichthyidae (*Hoplopteryx*, *Hoplostethus*) the supratemporal fossa extends forwards and the supraoccipital crest becomes elongated, thickened centrally and knife-edged. This trend continues further in the Berycidae, and *Beryx* has a long knife-edged crest, continued forwards by the frontals above the orbit, which resembles those of *Polymixia* and the carangids. If a " carangid-type " supraoccipital crest developed from an " *Aipichthys*-type " within the Berycoidei, there is no reason why these changes could not have occurred in other lineages.

It should also be mentioned here that Gosline (1966*a* : 410) has indicated that Beryciformes differ from Perciformes in the number of infraorbitals and the extent of the subocular shelf. He finds that in Beryciformes (except Holocentridae) there are four circumorbitals behind the lachrymal whereas in Perciformes there are five, and that in Beryciformes the subocular shelf extends over more than one infraorbital while in Perciformes it is confined to the second infraorbital. The subocular shelf extends along all the infraorbitals in Holocentridae (living and fossil) and in Polymixiidae (*Polymixia*, *Homonotichthys*), but in Trachichthyidae (living and fossil), Berycidae, Monocentridae, etc., the shelf is restricted to the second infraorbital, as in Perciformes. The subocular shelf also extends along all the infraorbitals in Anabantidae and Belontiidae (Liem 1963): probably a subocular shelf on all the infraorbitals, as in polymixiids, holocentrids and anabantids, is the primitive condition of the structure (Smith & Bailey 1962 : 3). In the number of infraorbitals the basic beryciform condition is undoubtedly as in percoids, with a total of six bones, a lachrymal, four infraorbitals, and a dermosphenotic overlying the autosphenotic: this condition occurs in Polymixiidae, living and fossil, and in living Holocentridae. In Trachichthyidae, Berycidae, Monocentridae and some Cretaceous Holocentridae (*Caproberyx*, *Stichocentrus*, Patterson 1964 : 347; 1967 : 89) the apparent reduction in number of circumorbital bones is caused by fusion of the dermo- and autosphenotics, which had already occurred in the Cretaceous trachichthyid *Hoplopteryx* (Patterson 1964, fig. 55).

In summary, of the various beryciform-perciform lineages which have been proposed, only the *Aipichthys*—carangid lineage emerges unscathed from a detailed examination of caudal structures. The caudal skeletons of Polymixiidae, *Sphenocephalus*, *Dinopteryx* and *Pycnosteroides* differ fundamentally from those of Perciformes in having a full neural spine on the second pre-ural centrum. In *Aipichthys* and *Pharmacichthys* there are tendencies towards the Perciformes in the occasional fusion of the second ural centrum with the preceding centrum and the occurrence of five hypurals, but it is only among the Berycoidei that the basal perciform caudal skeleton is duplicated. All known Berycoidei, even the very generalized *Lissoberyx*, are more specialized than Perciformes in having procurrent caudal spines, and this and characters of the skull (Patterson 1964 : 467) show that no perciform could have evolved from any known berycoid. But if the Perciformes and cognate groups (Channiformes, Scorpaeniformes, Pleuronectiformes, Tetraodontiformes) should prove to be a monophyletic group, an alternative to the traditional method—" an attempt first to define orders and other higher taxa and then to speculate upon their origin, albeit in the light of the known fossils " (Greenwood *et al.* 1966 : 346) is to use the criteria recommended by Hennig (1966 : 88, 120) and to search among the living fauna for the sister group (Hennig 1966 : 139; see also Brundin 1966 : 17) of this assemblage. A preliminary analysis suggests that the Berycoidei, not the Beryciformes as a whole, may fill this role. This is indicated not only by features of the caudal skeleton but by the fact that the Berycoidei is the only beryciform group showing such perciform features as a subocular shelf confined to the second infraorbital, the absence of epineurals, the pelvic girdle firmly joined to the cleithra (in Berycidae especially), pelvic fins containing a spine and five soft rays (in Anomalopidae and Gibberichthyidae, for example), partially separate soft and spinous dorsal fins, etc., and in the stephanoberycoids, which appear to be merely specialized offshoots of the trachichthyid lineage, loss of the orbitosphenoid. While it is clear that many of these perciform characters in Berycoidei have arisen independently within the group and were not inherited from a common ancestor of Berycoidei and perciforms, they appear to be true parallelisms (Simpson 1961 : 78), and are indicative of relationship.

(c) *Intermediate groups.*

Between the Beryciformes and the basal Percoidei, Greenwood *et al.* (1966 : 398) place the Zeiformes, Lampridiformes, Gasterosteiformes, Channiformes, Synbranchiformes, Scorpaeniformes, Dactylopteriformes and Pegasiformes. Of the Gasterosteiformes, Scorpaeniformes, Dactylopteriformes and Pegasiformes I have nothing to say. The Channiformes (see Gosline 1968) and Synbranchiformes are probably derived from the percoid level rather than from the beryciform or pre-beryciform.

In Zeiformes the caudal skeleton resembles those of basal Perciformes in having no free second ural centrum and in having only five hypurals, and is more advanced than basal percoids in having lost the second uroneural. In Zeidae (*Zeus*, *Cyttus*), Oreosomatidae (*Neocyttus*) and Grammicolepidae (*Xenolepidichthys*) there is a complete neural spine on the second pre-ural centrum, but this never occurs in conjunction with three epurals, and in Caproidae (*Capros*, *Antigonia*; Gosline 1961, fig. 4A), which in other respects appear to have the most primitive caudal skeletons of the group (the hypurals autogenous, the stegural autogenous in *Antigonia*) there are three epurals and there is a low crest on the second pre-ural centrum, as in percoids. Conditions in the Caproidae indicate that the neural spine on the second pre-ural centrum in Zeidae, Oreosomatidae and Grammicolepidae has arisen secondarily by fusion of the first epural (see above, p. 89, Fig. 28), and that as Gosline (1961) has already said, there is nothing in the caudal skeleton to distinguish Zeiformes from Perciformes. It has long been recognized that the Zeiformes are probably related to the Beryciformes, principally because of the pelvic ray count, but they also show many perciform features (Gosline 1961 : 36) and no conclusion has yet been reached on whether they are more closely related to the beryciforms or the perciforms, although in most recent classifications they are placed directly after the Beryciformes. Stinton (1967) has recently shown that there is a remarkable resemblance between the otoliths of *Antigonia* and those of Berycoidei (Berycidae, Trachichthyidae, and especially Monocentridae). Stinton interprets this as indicating that *Antigonia* is a berycoid, for he finds that the otoliths of *Capros* resemble those of the zeids rather than *Antigonia*. However, the evidence that *Antigonia* and *Capros* are related can hardly be ignored, and in Stinton's illustrations of zeiform otoliths it seems possible to recognize a trend in reduction and specialization of the otolith in the sequence *Antigonia–Capros–Cyttus–Zeus*: the same sequence of increasing specialization is also shown by fusion within the caudal skeleton. In my opinion Stinton's otolith evidence indicates not that *Antigonia* is a berycoid, but that as the most primitive living zeiform it retains the clearest evidence of a common ancestry with the Berycoidei. The percoid-like caudal skeleton, pelvic spine, etc., of the

Zeiformes do not oppose such a relationship. In Hennig's terminology, the Zeiformes appear to be the apomorph sister group of the Berycoidei, these two groups together forming the plesiomorph sister group of the perciform assemblage (see above, p. 95).

The Lampridiformes, previously unknown before the Oligocene, have recently acquired a respectable fossil record with Bonde's (1966) preliminary description of a ? veliferid from the basal Eocene Mo-clay of Denmark, his opinion that *Palaeocentrotus* Kühne (1941), from the same beds, is a lampridoid, not a zeiform, and the suggestion (p. 81) that the Danian *Bathysoma* is a lampridiform, not a menid. It appears that the deep-bodied Lampridiformes of the suborder Lampridoidei were an important element of early Tertiary faunas. The caudal skeleton of Lampridiformes (known in *Velifer, Lampris, Palaeocentrotus* and *Bathysoma*) is characterized by fusion of one or more of the upper hypurals with the second ural centrum, but in other respects it does not differ from that of Beryciformes (there are six hypurals in *Velifer*). In *Lampris* and *Velifer* the neural spine of the second pre-ural centrum is reduced, but in *Palaeocentrotus* (Kühne 1941, fig. 2) it is about half as long as its predecessor, a primitive condition only found among Beryciformes in *Aipichthys* (Fig. 11) and *Pharmacichthys*. Further, in *Lampris* and *Velifer* there are seventeen branched caudal rays and the caudal rays are deeply cleft basally, covering much of the hypurals. These points tend to confirm the suggestion (Patterson 1964 : 473) that the Lampridiformes are an offshoot of the Dinopterygoidei. Within the Dinopterygoidei, the second pre-ural neural spine, the seventeen branched principal rays, the " hypurostegy " and the absence of a pelvic spine all point to the Aipichthyidae and Pharmacichthyidae as ancestral forms.

Transference of *Bathysoma* to the Lampridiformes leaves unsettled the position of *Mene*, to which I thought *Bathysoma* was related (Patterson 1964 : 424). The similarities between *Mene* and *Bathysoma* are numerous, and extend to the form of the fin-rays, which are preserved in the middle part of the anal fin of the holotype of *B. lutkeni* in Copenhagen, and are short, broad and unbranched (Bonde, personal commn). The skull of *Mene* is also strikingly like that of *Velifer* (Regan 1907, figs. 167, 169). But the caudal skeletons of *Mene* and the Lampridiformes are very different. The six hypurals (in *Velifer*), fusion of the second ural centrum with the upper hypurals rather than with the preceding centrum, and the seventeen branched principal rays of Lampridiformes can only be derived from beryciform or pre-beryciform ancestors, but the caudal skeleton of *Mene*, with fifteen branched principal rays and fusion of the second ural centrum and first four hypurals with the preceding centrum could have evolved from the caudal skeleton of basal percoids (p. 81). Nor can I find anything in the skull and vertebral column of *Mene* which is against perciform ancestry. Nevertheless, *Mene* has an unusually long fossil record, extending back to the Lower Palaeocene. The earliest recorded species, *M. phosphaticus* Astre (1927) from the Montian of Tunisia, seems to agree with *Mene* rather than with the Lampridiformes in caudal structure. *Mene* is very common in the Middle Eocene of Monte Bolca: with *Mene* at Monte Bolca there occur other deep-bodied fishes of similar structure such as *Exellia* (= *Semiophorus*). These fishes, though poorly known, seem to agree with *Mene* in the absence of spines in the dorsal and anal fins (see Blot 1967 on *Exellia*) and also in the deeply cleft bases of the caudal fin-rays. It is difficult to know how much significance can be attached to this last character. E. & Y. Le Danois (1964), who coined the term " hypurostegy " for it, give great importance to it and use it to unite in an " ordre des Scombres " fishes as diverse as the holostean Pachycormidae, the Cretaceous Tselfatiidae, the lampridiform Veliferidae and Lampridae, the carangids, scombrids and others. In my opinion this assemblage is entirely spurious; the occurrence of hypurostegy in such varied groups indicates not that the fishes are related but that hypurostegy has arisen independently in a number of lines, for reasons as yet unknown. E. & Y. Le Danois made a new family Vomeridae to include *Mene*, the Eocene *Vomeropsis*, and the deep-bodied carangids *Vomer*, *Selene*, *Alectis* and *Hynnis*, grouping this family with the Lampridae, Veliferidae, Ephippidae and *Exellia*. Although the reasoning on which this grouping is made is doubtful, there may be some truth in it. It seems possible that *Mene* and *Exellia* could represent an independent attainment of the perciform grade from the Palaeocene lampridiform stock. But the possibility that the resemblances between these Eocene forms and the Lampridiformes are due to convergence is by no means ruled out: revisionary studies on the Monte Bolca fauna now in progress (Blot 1967) may settle this question.

IV. CONCLUSIONS

Study of a single structural complex such as the caudal skeleton is unlikely to produce firm conclusions on matters of phylogeny and relationships. Rather it will serve as a means of checking existing hypotheses and will raise questions to be settled by more comprehensive work. The main points arising from this paper are as follows. An asterisk indicates that the genus or group is extinct.

1. Ctenothrissiformes,* Myctophoidei and Beryciformes have a basically similar caudal skeleton, with the first ural and pre-ural centra fused, a free second ural centrum, a stegural (the first uroneural fused with neural arch material from the first ural and pre-ural centra), a second uroneural, three epurals and six hypurals. The primitive nineteen principal caudal rays are retained in all ctenothrissiforms and myctophoids, and in all beryciforms except the Polymixiidae, Sphenocephalidae,* Dinopterygidae * and Pycnosteroididae,* which have eighteen.

2. Ctenothrissiformes * (*Aulolepis*, *Ctenothrissa*) and Myctophoidei (*Aulopus*, *Nematonotus*,* *Sardinioides*,* *Acrognathus* *) have a large caudal scute above and below the caudal skeleton. The myctophoids *Nematonotus* * and *Sardinioides attenuatus* * have a single urodermal on the base of the upper caudal rays. Both caudal scutes and urodermals are relict structures absent in all higher groups.

3. The neural spine of the second pre-ural centrum in teleosts is primitively slender and about half as long as its predecessor, as in *Elops* and *Leptolepis*.* This type of second pre-ural neural spine persists in the myctophoids *Aulopus* and *Nematonotus* * and in the beryciforms *Aipichthys* * and *Pharmacichthys*.* In Ctenothrissiformes,* *Ctenothrissa* and *Aulolepis* have this short spine expanded into a plate, as it is in most myctophoids, but in *Pateroperca* the spine is elongate and supports procurrent fin-rays. A fully developed second pre-ural neural spine also occurs among Beryciformes in all polymixioids (Polymixiidae, Sphenocephalidae*) and in the dinop-

terygoids *Dinopteryx** and *Pycnosteroides.** In Berycoidei, as in generalized Perciformes, the second pre-ural neural arch and spine are reduced to a low crest.

4. The differences between the caudal skeletons of Myctophoidei and Ctenothrissiformes* and those of the most primitive teleosts are minor. Among primitive teleosts the Clupavidae * come closest to the Ctenothrissiformes and Myctophoidei in caudal anatomy.

5. The foremost procurrent caudal fin-rays are spinous in all living Beryciformes. This is a feature peculiar to Beryciformes: Perciformes appear to be without procurrent caudal spines. Procurrent caudal spines also occur in some species of *Ctenothrissa* and in *Aulolepis* (Ctenothrissiformes*), probably an indication of relationship between Ctenothrissiformes and Beryciformes, although procurrent caudal spines have also developed in advanced members of the myctophoid family Myctophidae. Among Cretaceous Beryciformes, procurrent caudal spines occur only in forms already known to be closely related to living Beryciformes (all Berycoidei and the polymixiids *Homonotichthys** and *Pycnosterinx**) and in *Dinopteryx.**

6. Within the Beryciformes, the principal variations in the caudal skeleton and fin (apart from those in the second pre-ural neural spine, principal fin-ray count and procurrent fin-rays already mentioned) are the presence of only two epurals in *Sphenocephalus** (Polymixioidei), the presence of only five hypurals in *Aipichthys velifer,** some specimens of *Pycnosteroides** (both Dinopterygoidei) and in many Berycoidei (living holocentrids, *Diretmus*), and the fusion of the second ural centrum with the preceding centrum in some specimens of *Aipichthys** and in many Berycoidei (Berycidae, Diretmidae, Anoplogasteridae, living Holocentridae). A full neural spine on the second pre-ural centrum has been found in one individual of *Aipichthys** and one of *Monocentris*, simulating the polymixoid condition.

7. The basal perciform caudal skeleton differs from the basal beryciform type in having only five hypurals, no free second ural centrum and only seventeen principal rays. Perciformes are primitively characterized by having a low neural crest on the second pre-ural centrum. Where a complete second pre-ural neural spine occurs as a normal feature in perciform or higher groups the condition is secondary, the spine representing an epural which has secondarily fused with the neural arch.

8. Evidence from the caudal skeleton does not support the various independent beryciform—perciform lineages which have been proposed. The polymixioids and the dinopterygoids *Dinopteryx** and *Pycnosteroides** differ fundamentally from the various perciform groups which they otherwise resemble in having a fully developed neural spine on the second pre-ural centrum. *Pharmacichthys,** which resembles the acanthuroids and balistoids in many ways, differs from them in having the bases of the caudal fin-rays deeply cleft, and is therefore unlikely to have been ancestral to these groups. Only the postulated link between *Aipichthys** and the carangids is not opposed by evidence from the caudal skeleton and fin.

9. Although no known berycoid could have been ancestral to any perciform, the Berycoidei is the only beryciform group in which the caudal skeleton evolves towards the percoid condition. There are many other characters and evolutionary trends in which the Berycoidei is the only beryciform group to resemble the percoids: these suggest that the Berycoidei is the sister group of the Perciformes and cognate groups.

10. The caudal skeleton shows that the Danian *Bathysoma** is a lampridiform (the earliest yet known), not a member of the Menidae. It is suggested that the Lampridiformes originated from near the beryciform families Aipichthyidae* and Pharmacicthyidae.* In the Eocene there are fishes (*Mene*, *Exellia**) which have reached the perciform grade but resemble the Palaeocene and Eocene Lampridiformes: possibly these forms represent an independent attainment of the perciform grade from lampridiform ancestors.

11. The caudal skeleton of the Zeiformes is basically of percoid type, but the evidence of zeiform otoliths indicates that they are closely related to the Berycoidei. The Zeiformes is evidently the sister group of the Berycoidei, these two groups together being the sister group of the perciform assemblage.

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VI. ABBREVIATIONS USED IN FIGURES

d2	second uroneural
e 1–3	epurals
f.s	caudal scute
h 1–6	hypurals
hpu2	haemal spine of second pre-ural centrum
npu2, npu3	neural spines of second and third pre-ural centra
ph	parhypural (haemal spine of first pre-ural centrum)
pu1 + u1	centrum formed by fusion of first pre-ural and ural centra
pu2, pu3, pu4	second, third and fourth pre-ural centra
st	stegural (first uroneural fused with pre-ural neural arch material)
u2	second ural centrum

Combinations of symbols linked by plus signs indicate compound elements formed by fusion of the bones indicated.

BRITISH M... 18 NOV 1968 NATURAL HISTORY

PRINTED IN GREAT BRITAIN
BY ADLARD & SON LIMITED
BARTHOLOMEW PRESS, DORKING

17 JAN
NATURAL HISTORY

NON-CALCAREOUS MICROPLANKTON FROM THE CENOMANIAN OF ENGLAND, NORTHERN FRANCE AND NORTH AMERICA

PART I

R. J. DAVEY

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
GEOLOGY Vol. 17 No. 3
LONDON: 1969

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Pp. 103–180; 11 *Plates*; 16 *Text-figures*

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THE BULLETIN OF THE BRITISH MUSEUM (NATURAL HISTORY), *instituted in* 1949, *is issued in five series corresponding to the Departments of the Museum, and an Historical series.*

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In 1965 *a separate supplementary series of longer papers was instituted, numbered serially for each Department.*

This paper is Vol. 17, *No.* 3 *of the Geological (Palaeontological) series. The abbreviated titles of periodicals cited follow those of the World List of Scientific Periodicals.*

World List abbreviation:
Bull. Br. Mus. nat. Hist. (Geol.)

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TRUSTEES OF
THE BRITISH MUSEUM (NATURAL HISTORY)

Issued 17 *January*, 1969 *Price* £2 16s,

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Manuscript accepted May 1967

CONTENTS

Page
Synopsis . . . 107
I. Introduction . . . 107
  Acknowledgments . . . 110
II. Stratigraphic Location of Samples . . . 112
  Fetcham Mill Borehole . . . 112
  Compton Bay . . . 112
  Speeton . . . 112
  Hunstanton . . . 115
  Devon . . . 115
  Escalles Borehole . . . 115
  Saskatchewan . . . 115
  Texas . . . 115
III. Systematic Descriptions . . . 120
  Genus *Gonyaulacysta* Deflandre . . . 120
    Gonyaulacysta cassidata (Eisenack & Cookson) . . . 120
      whitei Sarjeant . . . 120
      fetchamensis Sarjeant . . . 120
      exilicristata sp. nov. . . . 121
      delicata sp. nov. . . . 123
      sp. A. . . . 124
  Genus *Cribroperidinium* Neale & Sarjeant . . . 125
    Cribroperidinium intricatum sp. nov. . . . 125
    Other species . . . 128
    Cribroperidinium orthoceras (Eisenack) . . . 128
  Genus *Carpodinium* Cookson & Eisenack . . . 129
    Carpodinium obliquicostatum Cookson & Hughes . . . 129
  Genus *Ellipsodinium* Clarke & Verdier . . . 129
    Ellipsodinium rugulosum Clarke & Verdier . . . 130
  Genus *Apteodinium* Eisenack . . . 130
    Apteodinium granulatum Eisenack . . . 130
  Genus *Trichodinium* Eisenack & Cookson . . . 131
    Trichodinium castaneum (Deflandre) . . . 131
  Genus *Microdinium* Cookson & Eisenack . . . 132
    Microdinium cf. *ornatum* Cookson & Eisenack . . . 132
      setosum Sarjeant . . . 133
      distinctum sp. nov. . . . 133
      variospinum sp. nov. . . . 135
      veligerum (Deflandre) . . . 136
      crinitum sp. nov. . . . 137

- Genus *Histiocysta* nov. 138
  - *Histiocysta palla* sp. nov. 138
- Genus *Fromea* Cookson & Eisenack 140
  - *Fromea amphora* Cookson & Eisenack 140
- Genus *Chytroeisphaeridia* Sarjeant 140
  - *Chytroeisphaeridia euteiches* sp. nov. 141
- Genus *Cassiculosphaeridia* nov. 141
  - *Cassiculosphaeridia reticulata* sp. nov. 142
- Genus *Epelidosphaeridia* nov. 142
  - *Epelidosphaeridia spinosa* (Cookson & Hughes) . . . 143
- Genus *Hystrichosphaeridium* Deflandre 143
  - *Hystrichosphaeridium tubiferum* (Ehrenberg) . . . 143
    - *deanei* Davey & Williams . . . 144
    - *readei* Davey & Williams . . . 144
    - *radiculatum* Davey & Williams . . 144
    - *mantelli* Davey & Williams . . 145
    - *bowerbanki* Davey & Williams . . 145
    - *difficile* Manum & Cookson . . . 145
- Genus *Oligosphaeridium* Davey & Williams 146
  - *Oligosphaeridium complex* (White) 146
    - *reticulatum* Davey & Williams . . . 147
    - *prolixispinosum* Davey & Williams . . 147
    - *anthophorum* (Cookson & Eisenack) . . 147
    - *reniforme* (Tasch) 148
- Genus *Litosphaeridium* Davey & Williams 148
  - *Litosphaeridium siphoniphorum* (Cookson & Eisenack) . . 148
- Genus *Polysphaeridium* Davey & Williams 151
  - *Polysphaeridium pumilum* Davey & Williams . . . 151
    - *laminaspinosum* Davey & Williams . . 151
- Genus *Tanyosphaeridium* Davey & Williams 151
  - *Tanyosphaeridium variecalamum* Davey & Williams . . 151
- Genus *Callaiosphaeridium* Davey & Williams 151
  - *Callaiosphaeridium asymmetricum* (Deflandre & Courteville) . 152
- Genus *Cleistosphaeridium* Davey, Downie, Sarjeant & Williams 152
  - *Cleistosphaeridium heteracanthum* (Deflandre & Cookson) . 152
    - *multifurcatum* (Deflandre) . . . 152
    - *armatum* (Deflandre) 153
    - *polypes* (Cookson & Eisenack) . . . 154
    - var. *clavulum* nov. 154
    - *huguonioti* (Valensi) 155
    - var. *pertusum* nov. 156
    - *flexuosum* Davey, Downie, Sarjeant & Williams 157
    - *parvum* sp. nov. 157
    - *aciculare* sp. nov. 158
- Genus *Surculosphaeridium* Davey, Downie, Sarjeant & Williams 158
  - *Surculosphaeridium longifurcatum* (Firtion) 158
- Genus *Hystrichokolpoma* Klumpp 159
  - *Hystrichokolpoma ferox* (Deflandre) 159
- Genus *Prolixosphaeridium* Davey, Downie, Sarjeant & Williams 160
  - *Prolixosphaeridium conulum* sp. nov. 160
- Genus *Coronifera* Cookson & Eisenack 161
  - *Coronifera oceanica* Cookson & Eisenack 162

Genus *Exochosphaeridium* Davey, Downie, Sarjeant & Williams . . . 162
Exochosphaeridium phragmites Davey *et al.* 163
pseudohystrichodinium (Deflandre) . . . 163
striolatum (Deflandre) 164
var. *truncatum* nov. 164
Other species 166
Genus *Cyclonephelium* Deflandre & Cookson 166
Cyclonephelium distinctum Deflandre & Cookson . . . 166
membraniphorum Cookson & Eisenack . . . 167
vannophorum sp. nov. 168
paucispinum sp. nov. 170
eisenacki sp. nov. 170
Genus *Adnatosphaeridium* Williams & Downie 171
Adnatosphaeridium chonetum (Cookson & Eisenack) . . . 171
Genus *Hystrichosphaera* O. Wetzel 172
Hystrichosphaera ramosa (Ehrenberg) 172
var. *ramosa* (Ehrenberg) 172
var. *gracilis* Davey & Williams 172
var. *multibrevis* Davey & Williams . . . 173
var. *reticulata* Davey & Williams . . . 173
cingulata (O. Wetzel) 173
var. *reticulata* Davey & Williams . . . 174
crassimurata Davey & Williams 174
crassipellis Deflandre & Cookson . . . 174
Genus *Achomosphaera* Evitt. 174
Achomosphaera ramulifera (Deflandre) 174
sagena Davey & Williams 174
Genus *Hystrichodinium* Deflandre 174
Hystrichodinium voigti (Alberti) 175
dasys sp. nov. 175
IV. References 176

SYNOPSIS

This paper, which will appear in two parts, presents the results of a detailed study of some non-calcareous microplankton from the Upper Cretaceous, and in particular of assemblages of Cenomanian age. The stratigraphical potentialities of the fossil microplankton are briefly assessed by the analysis of samples from five localities in England and one in France. To assess the potentialities of long-range correlation, assemblages from Saskatchewan and Texas have also been examined. Both quantitative and qualitative methods have been employed and the correlations, both intra- and inter-regional, are promising. Seven new genera and thirty-five new species and varieties are described.

I. INTRODUCTION

Fossil non-calcareous microplankton consist mainly of cysts of dinoflagellates, together with various forms of unknown affinity placed in the Group Acritarcha Evitt (1963). The majority of dinoflagellates are free-living, oceanic and planktonic. They have a complex life-cycle, usually composed of four stages, in one of which (the motile stage) they are capable of limited vertical movement by the use of two flagella. During the life cycle, if the organism is subject to adverse conditions, a resting cyst is formed. This, most palynologists believe, is the only stage in the dinoflagellate life-cycle preserved in the fossil state. Fossil non-calcareous microplankton are useful as stratigraphic indices because they are planktonic, of relatively resistant composition, abundant in most marine sedimentary samples, and easy to extract. Hence the principal object of the study was to assess how accurate dinoflagellate cysts are for intra- and inter-regional stratigraphic correlations.

The order of description of the dinoflagellate cyst-families follows that in Sarjeant

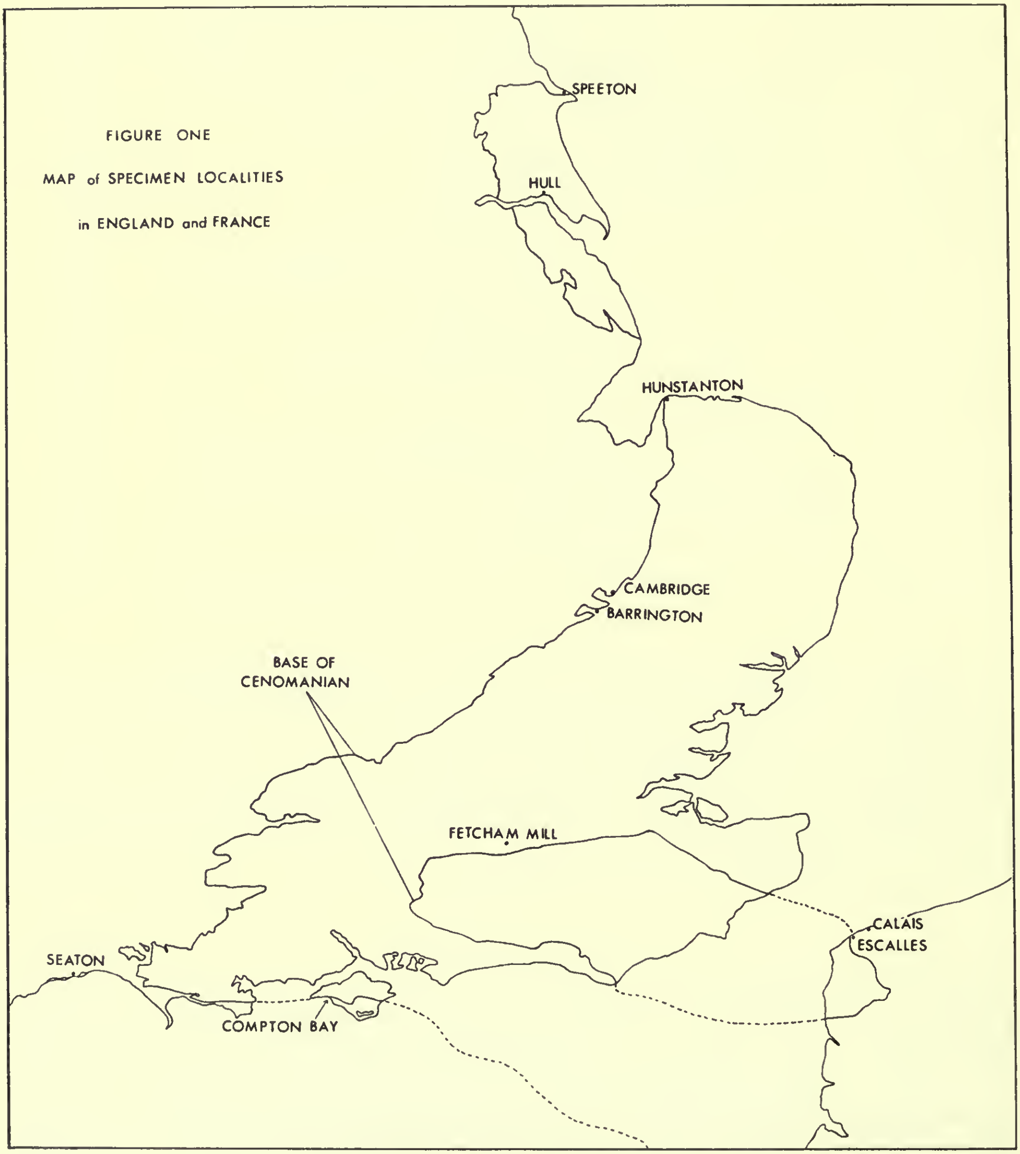
FIGURE ONE
MAP of SPECIMEN LOCALITIES
in ENGLAND and FRANCE
SPEETON
HULL
HUNSTANTON
CAMBRIDGE
BARRINGTON
BASE OF CENOMANIAN
FETCHAM MILL
SEATON
COMPTON BAY
CALAIS
ESCALLES

Fig. 1. Map of specimen Localities in England and France.

& Downie (1966). The adjectives used when describing the frequency of a species in an assemblage have been defined as follows:—

Very Common	10–100%
Common	1–10%
Infrequent	0·1–1%
Rare	0·01–0·1%
Very Rare	under 0·01%

The first fossil microplankton were described and figured by Ehrenberg (1838, 1843, 1854) and included forms embedded in flakes of Upper Cretaceous flint from Germany and Denmark. These observations stimulated English microscopists in the mid-nineteenth century into finding these organisms in English flints of the same age.

Little further research in this sphere was published until 1933 when O. Wetzel described assemblages from Upper Chalk flints of the Baltic region. In 1934 Deflandre published the first of a number of well illustrated papers dealing with fossil microplankton from the flints of the Paris Basin. Unfortunately the stratigraphic horizons of the flints are unknown, many being picked up in the streets of Paris. His two most important papers describing Upper Cretaceous microplankton were published in 1936 and 1937. They contain accurate figures and descriptions of many new species and genera mainly from the Senonian, although some of the flints are probably of Cenomanian and Turonian age.

Between 1936 and 1952 few papers dealing with microplankton from the Upper Cretaceous were published. Firtion (1952) described the first definite Cenomanian assemblage, the material having been obtained from the Lower Cenomanian of France. All his species have subsequently been observed in the Lower Chalk of England and France except for *Pareodina* sp. which is unidentifiable. Firtion's *Hystrichosphaeridium* cf. *salpingophorum* may correspond to *H. mantelli*, and *Micrhystridium ambiguum* is probably *Cleistosphaeridium huguonioti*.

Since 1955 a number of publications have been produced dealing mainly with the systematics of Cretaceous microplankton. Assemblages have been described from Germany by Gocht (1957, 1959), Eisenack (1958), and Alberti (1959, 1961), but only the latter author records Cenomanian species. Alberti (1961) described a series of assemblages from the Valanginian to Turonian of northern Germany. Eight species were recorded from the Cenomanian and all of these, except for *Korojonia dubiosa*, have been found during the present study. *Hystrichodinium pulchrum*, identified by Alberti from the Cenomanian, is here included within *Hystrichodinium voigti*. *Gonyaulax orthoceras*, figured by Alberti, is undoubtedly *Cribroperidinium intricatum* sp. nov., and *Palaeohystrichophora* cf. *paucisetosa* is probably a form of *P. infusorioides* possessing fewer spines than usual.

Lower Cretaceous assemblages were described by Neale & Sarjeant (1962), Pocock (1962), and Tasch, McClure & Oftedahl (1964). Górka (1963) described nine species of microplankton from the Cenomanian of Poland. All of these species have been found in the Cenomanian deposits of England and France, although some are considered to be incorrectly identified. *Gonyaulax orthoceras*, illustrated by Górka appears to be *Gonyaulacysta exilicristata* sp. nov. and her *Gonyaulax* sp. is probably *Cribroperidinium intricatum*; *Hystrichosphaeridium asterigerum* is probably equivalent to *Oligosphaeridium complex* and *Hystrichosphaeridium polytrichum* possibly to *Cleistosphaeridium armatum*. Her *Hystrichosphaeridium* cf. *striolatum* may also belong to the latter species.

Balteş (1963) described eight species of microplankton from the Cenomanian deposits of Roumania. Of these seven have been recorded in the present study. The species not recorded, *Ascodinium hialinium*, probably belongs to the genus *Deflandrea*. The identities of three other species are in doubt: some of the specimens illustrated as *Hystrichosphaeridium longifurcatum* probably belong to this species (transferred to *Surculosphaeridium* by Davey *et al.* 1966), but one specimen (pl. 7, fig. 12) probably belongs in *Hystrichosphaera*. *Histrichosphaeridium* sp. 22 resembles *Exochosphaeridium striolatum* var. *truncatum* nov. and *Hystrichosphaeridium* sp. 23 is possibly *Cleistosphaeridium multifurcatum*.

Manum & Cookson (1964) describe species of supposed lower Upper Cretaceous age from Arctic Canada and of these, eight have also been recorded from the Lower Chalk of England and France; however, the Arctic Canadian assemblages are more comparable to those obtained from Saskatchewan.

Cookson & Hughes (1964) gave the first account of microplankton from the deposits of Upper Albian and basal Cenomanian age in England. Thirty-three species were described from the Cenomanian and of these only six have not been recorded from the basal Cenomanian of Fetcham Mill (sample FM 840) and Compton Bay (CB 1).

A number of papers have been published (between 1954 and 1965) dealing with the microplankton of Australia and, in part, of New Guinea and Papua—Deflandre & Cookson (1954, 1955), Cookson (1956, 1965), Cookson & Eisenack (1958, 1960*a*, *b*, 1961, 1962*a*, *b*) Eisenack & Cookson (1960), and Cookson & Manum (1964). Unfortunately it is usually only possible to give the approximate age of the samples and, therefore, stratigraphic conclusions are not as meaningful as one would have hoped.

A number of species from the Cenomanian deposits of England were described by Davey, Downie, Sarjeant & Williams (1966) and the present paper published in two parts forms a natural continuation of that work.

Clarke & Verdier (1967) describe microplankton assemblages of Cenomanian to Senonian age from the Isle of Wight, southern England. The Cenomanian samples examined by them were obtained from a locality approximately sixteen miles to the east of Compton Bay. Their results indicated that the Upper Cretaceous could be divided into 5 zones and 5 subzones, and also into 7 " intervals " based on extinction points. The results concerning the Cenomanian are mainly substantiated in the present study.

ACKNOWLEDGMENTS

The research has been carried out during the tenure of a research studentship in the Department of Geology, The University of Nottingham.

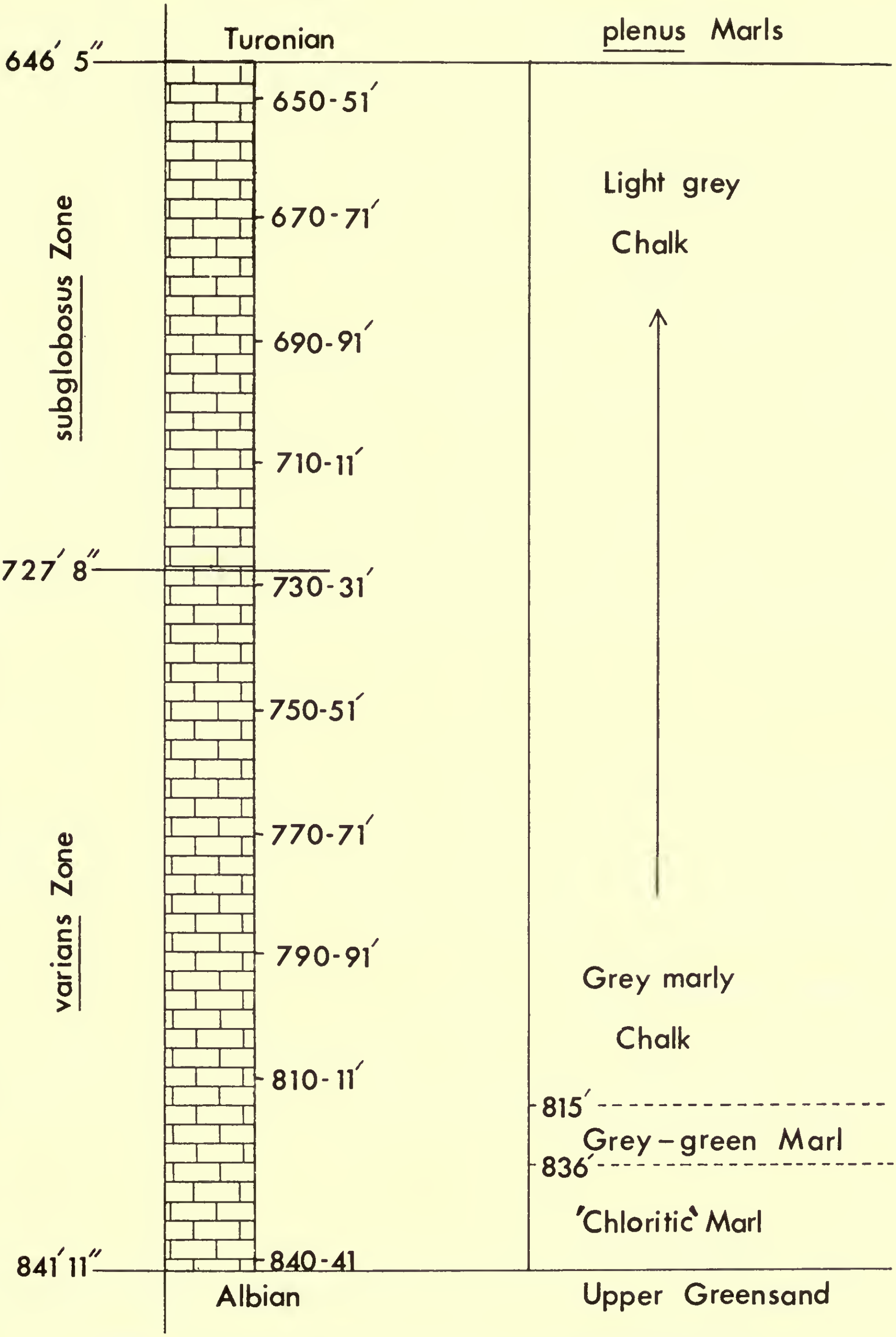
Turonian
plenus Marls
646′ 5″
650-51′
670-71′
690-91′
710-11′
727′ 8″
730-31′
750-51′
770-71′
790-91′
810-11′
840-41
841′ 11″
subglobosus Zone
varians Zone
Light grey Chalk
Grey marly Chalk
815′
Grey-green Marl
836′
'Chloritic' Marl
Albian
Upper Greensand

FIG. 2. Section showing the Location of the Samples analysed from Fetcham Mill, Surrey. Scale 1 inch to 30 feet.

The author would like to thank sincerely Dr. W. A. S. Sarjeant for considerable help and encouragement given at all stages during the course of this work, and also particularly acknowledges the interest and encouragement given by Professor W. D. Evans and Dr. A. J. Rowell. Thanks are due to Professor G. Deflandre for courtesy in entertaining the author and allowing him to examine type material at the Laboratoire de Micropaléontologie, École Practique des Hautes Études, Paris; and to Dr. G. L. Williams for his collaboration when dealing with the systematics of certain genera. The author is indebted to Mr. R. Hendry and his staff in the Department of Geology, The University of Nottingham for their assistance and provision of necessary laboratory equipment.

Special thanks are due to Sir James Stubblefield, former Director of the Institute of Geological Sciences, for permitting study of chalk samples from the Fetcham Mill Borehole; to the Bureau de Recherches Géologiques et Minières, for providing chalk samples from the Escalles Borehole; to the Department of Mineral Resources, Saskatchewan, for providing Cretaceous samples from the International Yarbo Borehole no. 17; to Dr. J. D. Powell, for providing Upper Cretaceous samples from Texas; to Dr. W. E. Smith, for providing samples from the Cenomanian of south Devon; and to Dr. K. Diebel, of the Institut für Paläeontologie, Humboldt University, East Berlin, for courteously permitting the loan of Ehrenberg's holotypes.

The following abbreviations are used in the text: B.M. (N.H.)—British Museum (Natural History): G.S.M.—Institute of Geological Sciences, London.

II. STRATIGRAPHIC LOCATION OF SAMPLES

1. **Fetcham Mill Borehole,** Leatherhead, Surrey (TQ 15815650).

This borehole has been described by Gray (1965). Ten samples at 20-foot intervals were processed from the Cenomanian (Lower Chalk) succession (Fig. 2). In addition one sample from the Albian (Upper Greensand) and one from the Turonian (Middle Chalk) were analysed for comparative purposes.

2. **Compton Bay,** Isle of Wight (SZ 365854)

The Cenomanian is well exposed in the cliff section at this locality and has been described by Jukes Browne (1903) and Osborne White (1921). Samples were collected at 7–8 ft. intervals and eleven samples, at approximately 14 ft. intervals, were analysed for their organic-shelled microplankton content (Fig. 3).

3. **Speeton,** Yorkshire (TA/166750)

The Cenomanian succession is fully exposed in the cliffs at Speeton. The base of this stage was taken to coincide with the bottom of bed V (Wright 1963) which, together with the overlying bed U, is placed in the Red Chalk (Fig. 4). The succession has been described recently by Kaye (1964). Seven samples were collected and analysed for their microplankton content.

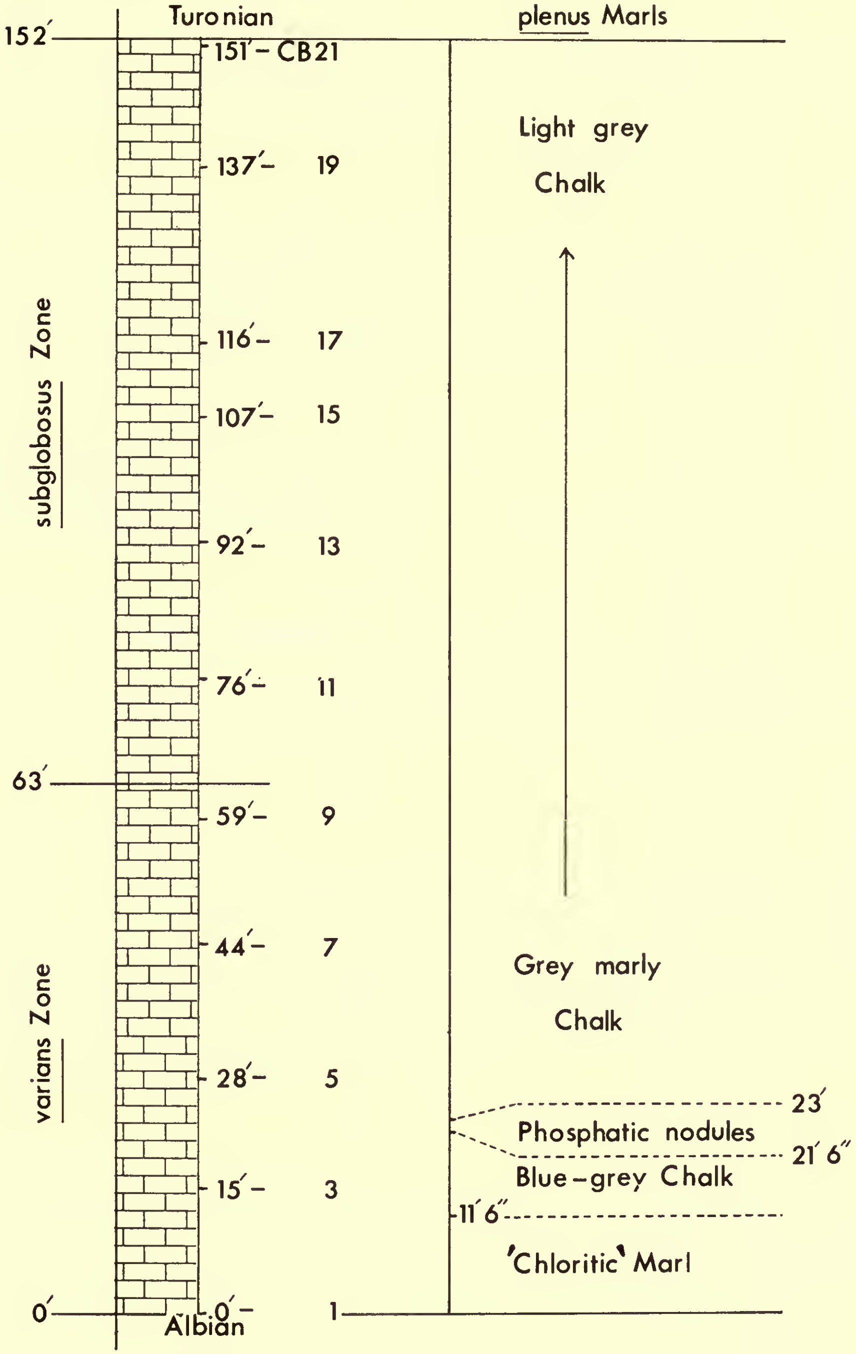
Turonian
plenus Marls
152′
151′ – CB21
137′ – 19
116′ – 17
107′ – 15
92′ – 13
76′ – 11
63′
59′ – 9
44′ – 7
28′ – 5
15′ – 3
0′
0′ – 1
Albian
subglobosus Zone
varians Zone
Light grey Chalk
Grey marly Chalk
23′
Phosphatic nodules
21′ 6″
Blue-grey Chalk
11′ 6″
'Chloritic' Marl

FIG. 3. Section showing the Location of the Samples analysed from Compton Bay, Isle of Wight. Scale 1 inch to 20 feet.

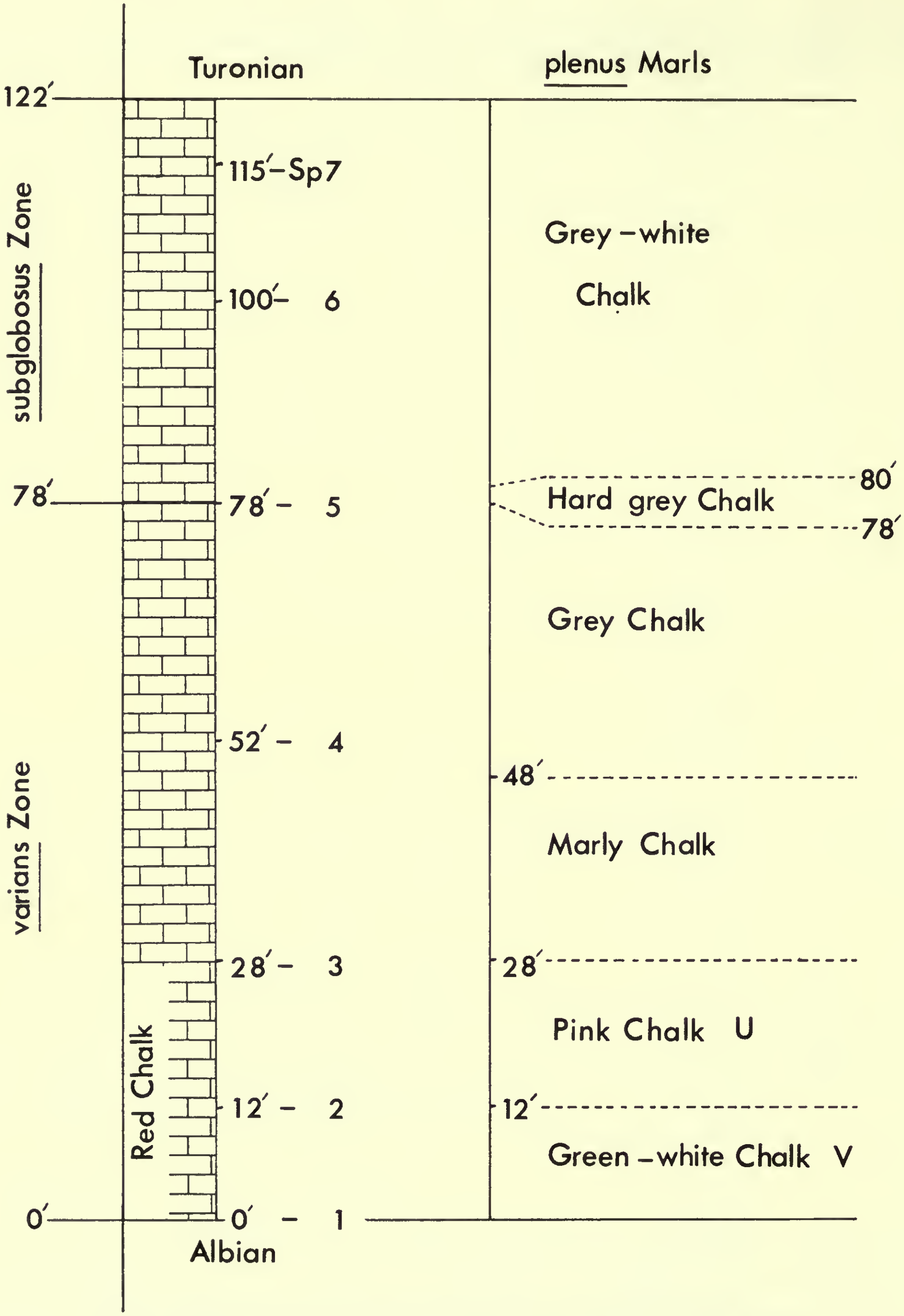
Turonian
plenus Marls
122′
115′–Sp7
subglobosus Zone
Grey–white
Chalk
100′– 6
80′
Hard grey Chalk
78′
78′ – 5
78′
Grey Chalk
52′ – 4
48′
varians Zone
Marly Chalk
28′ – 3
28′
Pink Chalk U
Red Chalk
12′ – 2
12′
Green–white Chalk V
0′
0′ – 1
Albian

FIG. 4. Section showing the Location of the Samples analysed from Speeton, Yorkshire. Scale 1 inch to 20 feet.

4. **Hunstanton,** Norfolk. (TF 675420)

The *varians* and *subglobosus* zones are exposed in the Hunstanton cliffs (Peake & Hancock 1961). Three samples were processed, two from the lower zone and one from the base of the Totternhoe Stone (Fig. 5).

5. **Devon,** South Coast

The Cenomanian is represented between Salcombe and Lyme Regis by isolated patches composed of a few feet of sandy Cenomanian Limestone. These deposits were divided into four beds by Jukes-Browne (1903)—A1, A2, B and C. Bed C is probably the *Actinocamax plenus* Marls. The samples were collected from four localities by Dr. W. E. Smith (Fig. 6):

(i) *Maynards Cliff* (see Smith 1961 : 114)
(ii) *Beer Head* (see Smith 1957 : 123)
(iii) *Whitecliff* (see Smith 1957 : 118)
(iv) *Humble Point* (see Smith 1965 : 126)

6. **Escalles Borehole,** Cap Blanc-Nez, Pas de Calais

The borehole, drilled by the Bureau de Recherches Géologiques et Minières in 1958 has been described by Destombes (1961). Eleven samples were obtained for analysis at about 20 ft. (6m.) intervals (Fig. 7).

7. **Saskatchewan,** south-east

The borehole, from which the Saskatchewan samples were obtained, was drilled for the Department of Mineral Resources, Saskatchewan and is called " International Yarbo, no. 17 ". It is located east of Regina at Lsd. 1, Sec. 24, Twp. 20, Rg. 33, W1st Meridian. All depths are measured from the Kelly Bushing which is at an elevation of 1,690 ft. above sea level. Six samples of Albian/Cenomanian age were analysed for their microplankton content (Fig. 8).

8. **Texas,** north

Two samples were obtained from the Upper Cenomanian of north Texas (Tarrant County) for the author by Dr. J. D. Powell. The lower sample (T5) was obtained from the Upper Woodbine Formation (*Acanthoceras wintoni* Zone) and consists of a yellowish, slightly calcareous clay. The higher sample (T4) is from 35 ft. above the base of the Eagle Ford Formation (*Eucalycoceras* Zone). This is a thin-bedded yellow limestone containing shelly fossils and plant debris, in particular leaf fragments.

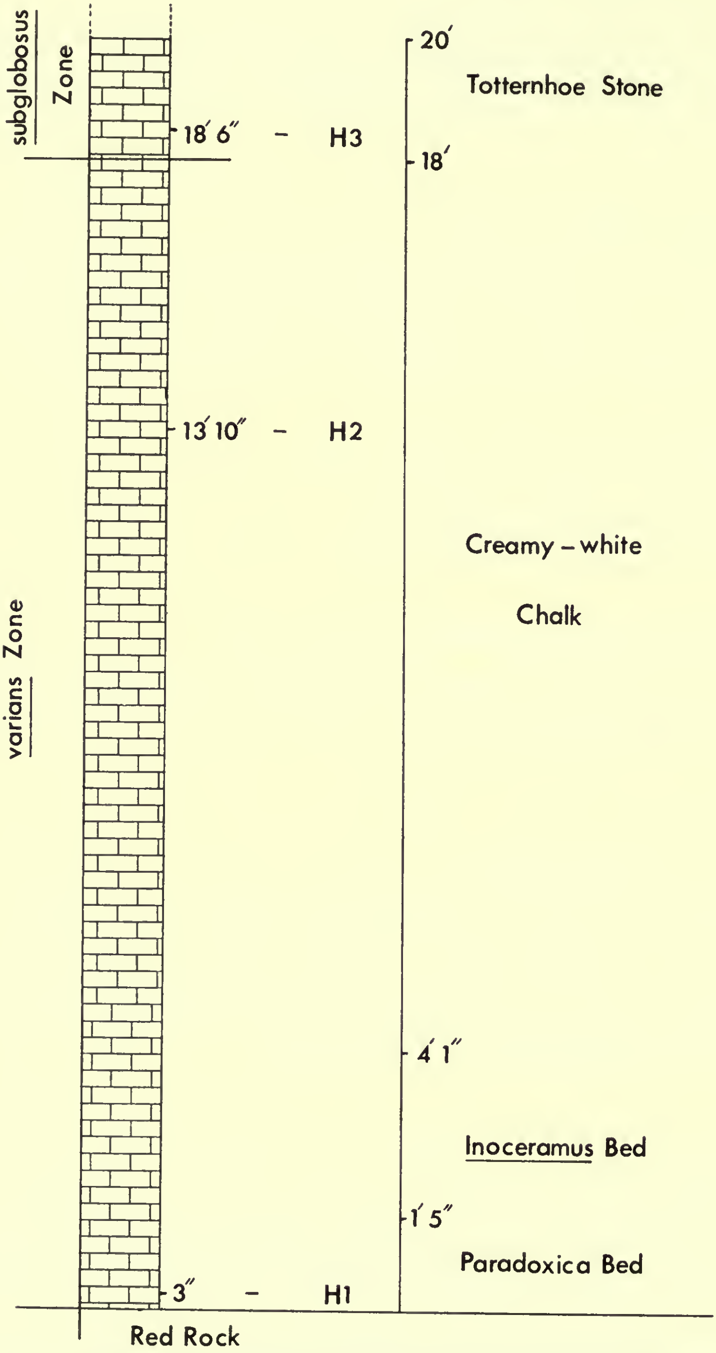
subglobosus Zone
varians Zone
18′ 6″ – H3
13′ 10″ – H2
3″ – H1
Red Rock
20′
Totternhoe Stone
18′
Creamy – white Chalk
4′ 1″
Inoceramus Bed
1′ 5″
Paradoxica Bed

FIG. 5. Section showing the Location of the Samples analysed from Hunstanton, Norfolk. Scale 1 inch to 2½ feet.

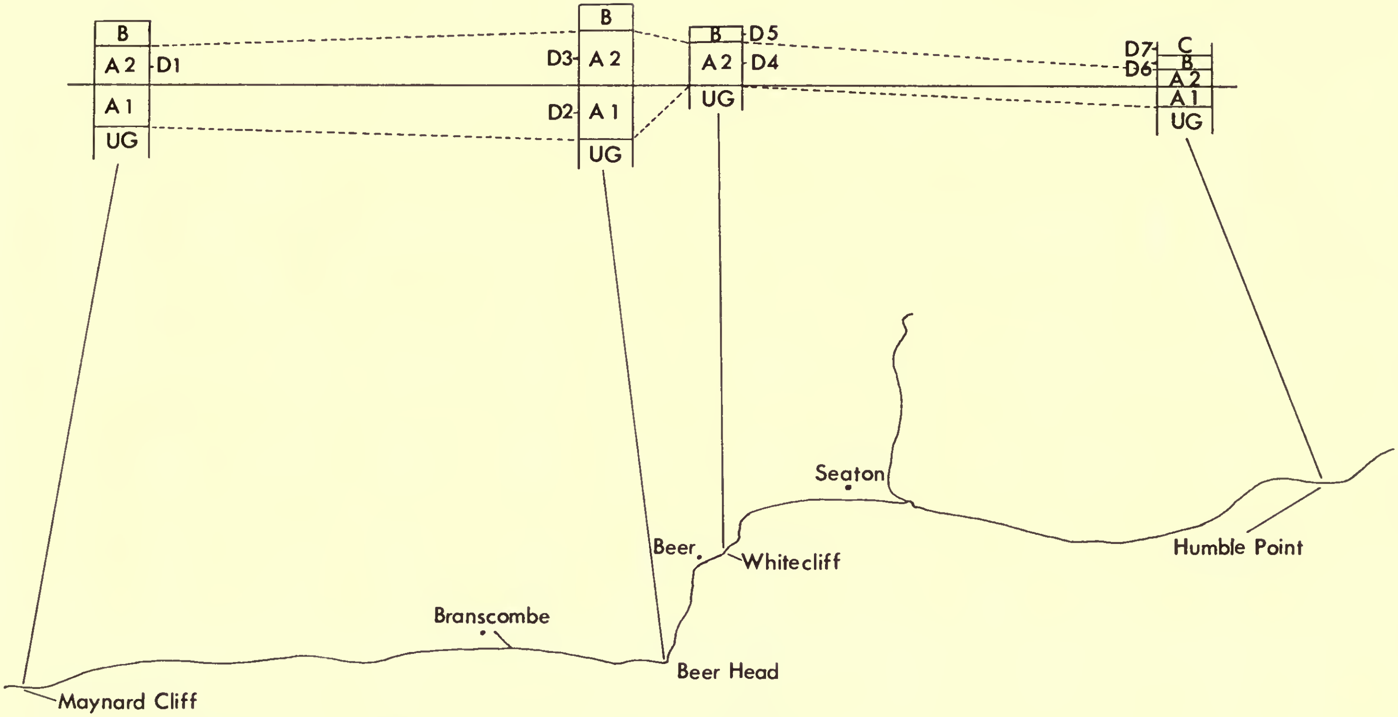
B
A 2
D1
A 1
UG
B
D3
A 2
D2
A 1
UG
B
D5
A 2
D4
UG
D7
D6
C
B
A 2
A 1
UG
Seaton
Beer
Whitecliff
Humble Point
Branscombe
Beer Head
Maynard Cliff

FIG. 6. Map and Section showing the Location of the Samples analysed from Devon (south coast). Scale 1 inch to 16 feet.

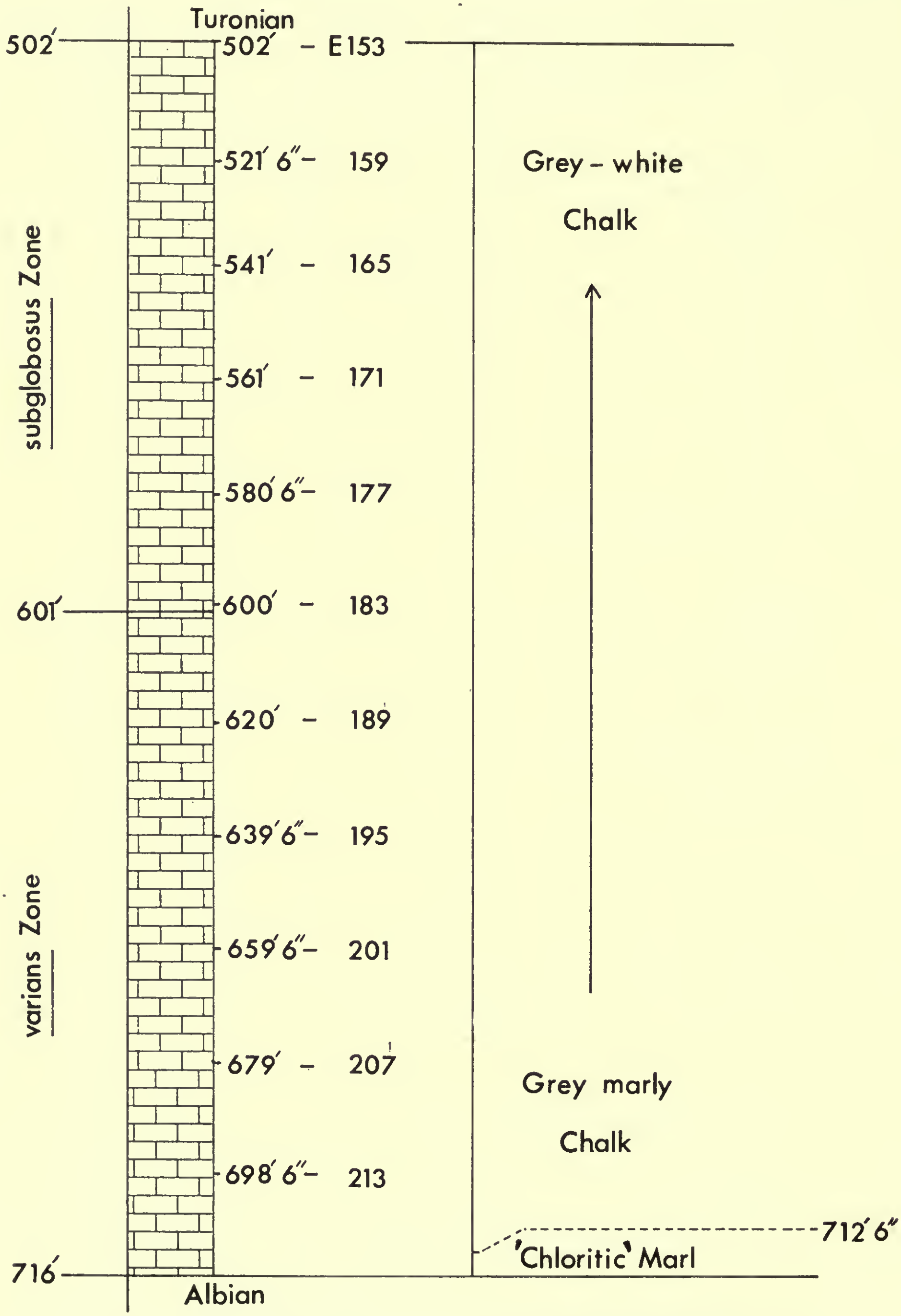
Turonian
502′
502′ – E153
521′ 6″– 159
541′ – 165
561′ – 171
580′ 6″– 177
601′
600′ – 183
620′ – 189
639′ 6″– 195
659′ 6″– 201
679′ – 207
698′ 6″– 213
716′
Albian
subglobosus Zone
varians Zone
Grey – white Chalk
Grey marly Chalk
'Chloritic' Marl
712′ 6″

FIG. 7. Section showing the Location of the Samples analysed from Escalles, France. Scale 1 inch to 30 feet.

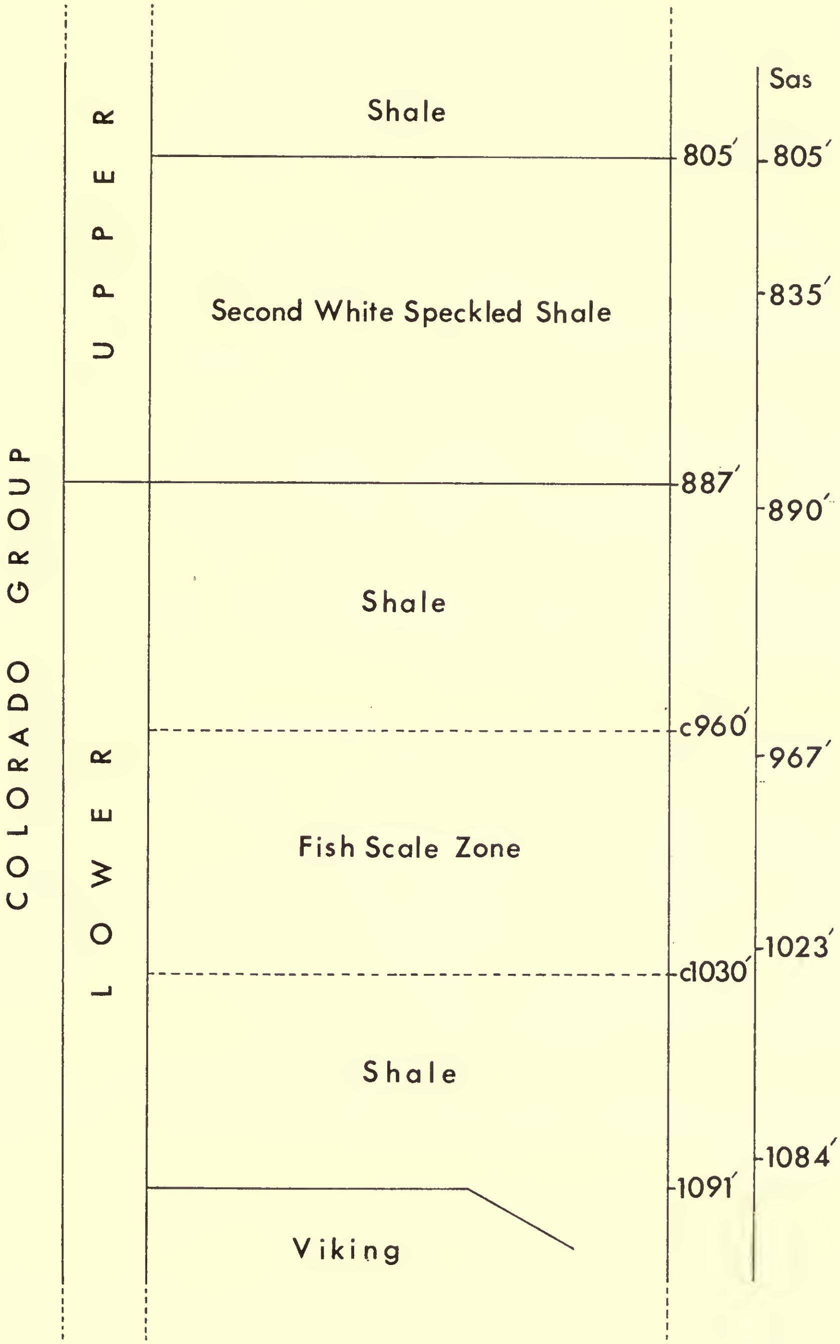
COLORADO GROUP
UPPER
LOWER
Shale
Second White Speckled Shale
Shale
Fish Scale Zone
Shale
Viking
805′
887′
c960′
c1030′
1091′
Sas
805′
835′
890′
967′
1023′
1084′

FIG. 8. Section showing the Location of the Samples analysed from Saskatchewan, Canada. Scale 1 inch to 50 feet.

III. SYSTEMATIC DESCRIPTIONS

Class *DINOPHYCEAE* Pasher

Subclass *DINIFEROPHYCIDAE* Bergh

Cyst-Family **GONYAULACYSTACEAE** Sarjeant & Downie 1966

Genus ***GONYAULACYSTA*** Deflandre emend. Sarjeant 1966

Gonyaulacysta cassidata (Eisenack & Cookson) emend. Sarjeant

1960 *Gonyaulax helicoidea* subsp. *cassidata* Eisenack & Cookson : 3, pl. 1, figs. 5, 6.
1966*a* *Gonyaulacysta cassidata* (Eisenack & Cookson) Sarjeant : 125, pl. 14, figs. 3, 4, text-fig. 31 (see also for earlier references).
1967 *Gonyaulacysta cassidata* (Eisenack & Cookson) Clark & Verdier: 29, pl. 4, figs. 4–6.

Dimensions. Range of observed specimens: overall length 59 (67·5) 78 μ, overall width 40 (46·4) 60 μ. Number of specimens measured, 14.

Remarks. The Cenomanian specimens examined are very similar to the Australian Aptian-Cenomanian forms of Eisenack & Cookson (1960) and Cookson & Eisenack (1962*b*) except that the former are slightly smaller in size.

Occurrence. *G. cassidata* is an infrequent species at all horizons throughout the Cenomanian of Fetcham Mill, Compton Bay and Escalles. It has not been recorded in the North American samples.

Gonyaulacysta whitei Sarjeant

1966*a* *Gonyaulacysta whitei* Sarjeant : 126, pl. 14, fig. 2, text-fig. 32.

Dimensions. Range of observed specimens: overall length 55–62 μ, overall width 42–50 μ. Number of specimens measured, 5.

Remarks. The shape of the shell, the tabulation and the crests make *G. whitei* an easily recognizable and distinctive species. *G.* cf. *ambigua* Cookson & Eisenack (1960*b*) from the Upper Jurassic is of the same shape and possesses similar crests and tabulation; plate 1'''' is absent. However, the apical horn of *G.* cf. *ambigua* is rudimentary or absent, thus making differentiation easy.

Occurrence. Of five specimens of *G. whitei* observed, four are from sample FM 770 and one from sample FM 750. The restricted distribution of this species and its similarity to *G.* cf. *ambigua* from the Upper Jurassic suggest the possibility that this is a derived form.

Gonyaulacysta fetchamensis Sarjeant

1966*a* *Gonyaulacysta fetchamensis* Sarjeant : 128, pl. 15, figs. 1, 2, text-fig. 33.

Remarks. *G. fetchamensis* has a rather unusual tabulation—two posterior intercalary plates and a seventh postcingular plate—and, as pointed out by Sarjeant (1966*a*), may subsequently form the basis of a new genus. As yet only two specimens have been studied and this species has, therefore, been placed in *Gonyaulacysta*. It appears to be a transitional type from the normal *Gonyaulacysta* to forms now placed in *Cribroperidinium* Neale & Sarjeant. The latter forms are of similar overall appearance but the shell is divided by low crests into an unusually large number of areas.

OCCURRENCE. *G. fetchamensis* is a rare species recorded only from the Chalk of H.M. Geological Survey borehole, Fetcham Mill, Surrey, at 840 ft. depth. Upper Cretaceous (Lower Cenomanian).

Gonyaulacysta exilicristata sp. nov.

(Pl. 1, figs. 1, 2; Figs. 9A, B)

DERIVATION OF NAME. Latin, *exilis*, thin or poor; *cristatus*, crested—with reference to the poorly defined sutural crests.

DIAGNOSIS. Shell subspherical; moderately well developed apical horn. Shell wall thick, finely but densely granular. Reflected tabulation 3′, 1a, 6″, 6c, 6‴ (—7‴?), 1 p, 1⁗. Plate boundaries marked by low, poorly defined crests which sometimes form small spines at crestal nodes. Cingulum narrow, weakly laevo-rotatory; sulcus of moderate width, widening slightly posteriorly.

HOLOTYPE. G.S.M. slide PF 3987 (1). Lower Chalk, H.M. Geological Survey Borehole, Fetcham Mill, Surrey at 730 ft. depth. Upper Cretaceous (Cenomanian).

DIMENSIONS. Holotype: overall length 83 μ, overall width 68 μ, length of horn 12 μ. Range: overall length 70 (81·6) 98 μ, overall width 58 (64·5) 71 μ. Number of specimens measured, 24.

DESCRIPTION. The shell wall measures between 2 and 3 μ in thickness, the endophragm being approximately twice as thick as the periphragm. The latter forms the apical horn which is triangular in cross-section due to the sutural ridges which delimit the apical plates extending along it. Lines of ornamentation, sometimes similar to the sutural crests, are present on some of the plates, particularly those in the postcingular series. Occasionally it appears that plate 4‴ is subdivided by a low ridge so giving seven postcingular plates.

The cingulum is fairly narrow (3 to 4 μ) and only slightly laevo-rotatory. The sulcus often possesses a posterior ventral plate. In the medial-posterior part of the furrow there is usually an elongate depression, as seen in the holotype (Fig. 9A). A precingular archaeopyle is typically present.

REMARKS. *G. exilicristata* sp. nov. is distinguished from all previously described species by its overall shape, the type of plate boundaries and the tabulation. *Apteodinium granulatum* Eisenack (1958) is similar but has a stouter apical horn and a tabulation appears to be absent; the cingulum is only rarely visible.

Cribroperidinium orthoceras (Eisenack) comb. nov. is also similar but possesses a longer apical horn, and the tabulation differs and is more clearly defined.

OCCURRENCE *G. exilicristata* is a rare species recorded from a number of horizons throughout the Cenomanian of Fetcham Mill, Compton Bay and Escalles. At only one horizon is this species common, in sample FM 730 from Fetcham Mill. Two specimens have been recorded from Saskatchewan, both from sample Sas 1084.

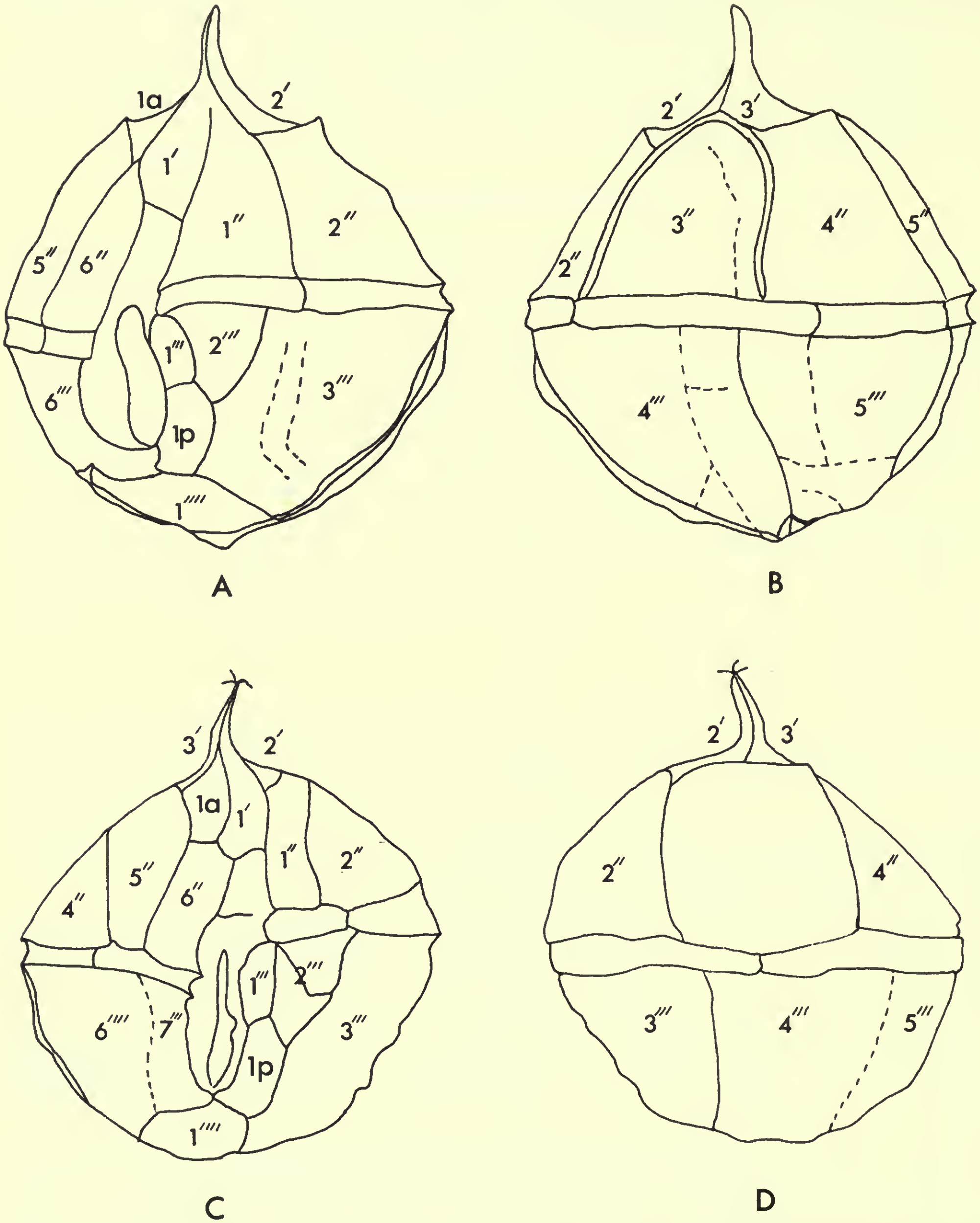
1a
2'
1'
1''
2''
5''
6''
1'''
2'''
3'''
6'''
1p
1''''
A
2'
3'
3''
4''
5''
2''
4'''
5'''
B
3'
2'
1a
1'
1''
2''
4''
5''
6''
6''''
7'''
1'''
2'''
3'''
1p
1''''
C
2'
3'
2''
4''
3'''
4'''
5'''
D

FIG. 9. *Gonyaulacysta exilicristata* sp. nov., A. Ventral Surface of Holotype (× 900), B. Dorsal Surface of Holotype, (× 900). *Gonyaulacysta* Sp. A., C. Ventral Surface slide PF. 3987 (2) (× 900). D. Dorsal Surface slide PF. 3987 (2) (× 900).

Gonyaulacysta delicata sp. nov.

(Pl. 1, figs. 7, 8; Figs. 10A, B)

DERIVATION OF NAME. Latin, *delicatus*, delicate—with reference to the delicate nature of the shell.

DIAGNOSIS. Shell subspherical, epitract and hypotract of similar size. Shell wall thin, smooth. Apical horn absent, there being a small circular apical plate in this position surrounded by three large apical plates. Reflected tabulation 4′, 1a, 6″, 6c, 6‴, 1p, 1⁗. Plate boundaries well defined by low crests. Cingulum wide, strongly laevo-rotatory; sulcus broad.

HOLOTYPE. B.M. (N.H.) V. 51979(1). Lower Colorado, Second White Speckled Shale, International Yarbo Borehole No. 17, Saskatchewan at 835 ft. depth. Upper Cretaceous (Cenomanian).

PARATYPE. B.M. (N.H.) V. 51979(2).

DIMENSIONS. Holotype: length of shell 57 μ, width 51 μ. Paratype: length of shell 55 μ, width 47 μ. Range: length of shell 52–60 μ, width 47–51 μ. Number of specimens measured, 4.

DESCRIPTION. The shell wall is very thin (less than 0·5 μ thick) and only attains a thickness of 0·5 μ when forming the plate boundaries. Due to the thinness of the shell wall specimens are easily distorted. The tabulation has, however, been formulated after the examination of a number of specimens.

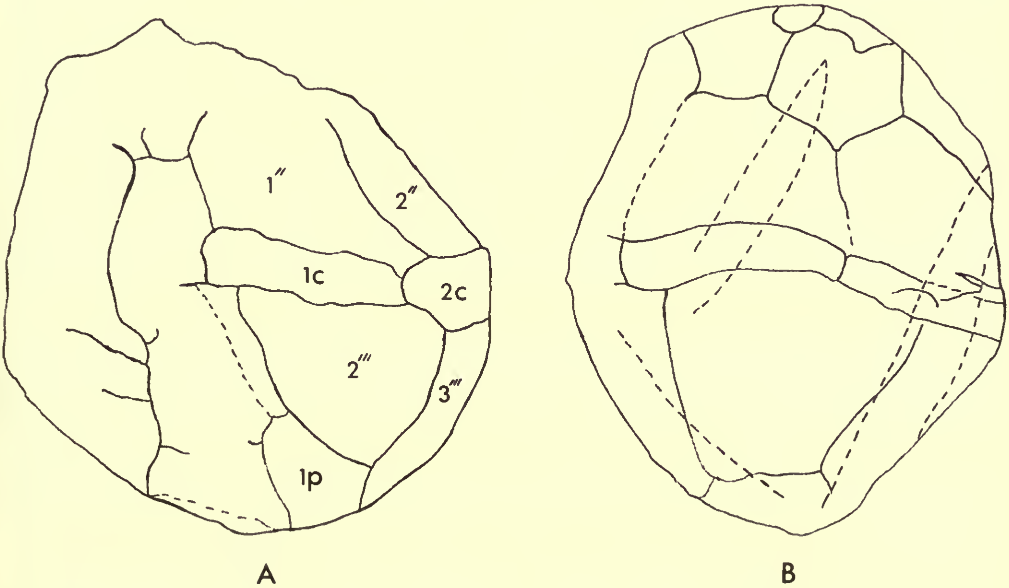

FIG. 10. *Gonyaulacysta delicata* sp. nov., A. Ventral surface of Holotype (× 1500). B. Dorsal surface of Holotype (× 1500).

Anteriorly three apical plates (2′, 3′ and 4′) abutt against a small circular plate, plate 1′, which is in the position normally occupied by the apical horn. The precingular and postcingular series of plates are large and more or less pentagonal. Plate 3″ is always lost in archaeopyle formation. The first postcingular plate is elongate and has a poorly defined sulcal border.

The cingulum is wide (4 to 7 μ) and tends to be constricted at the cingular plate boundaries. The sulcus is broad and widens slightly towards the posterior. The anterior end of the sulcus has a flat margin from which arise plates 1′ and 1a. At the posterior end of the sulcus there may be developed a posterior ventral plate.

REMARKS. The presence of very low sutural crests, the lack of an apical horn and the tabulation differentiate *G. delicata* sp. nov. from all previously described species. *G. ambigua* Deflandre, from the Kimeridgian of France, is of similar appearance but possesses a small apical horn and differs in tabulation detail.

OCCURRENCE. *G. delicata* has been found in only one sample, Sas 835, and it is there infrequent. This restricted distribution may well indicate that this is a derived species.

Gonyaulacysta sp. A.

(Pl. 1, figs. 9, 10; Figs. 9C, D)

DESCRIPTION. Only one well preserved specimen of this species has so far been observed. It possesses a subspherical shell, bearing a moderately well developed horn with a trifid termination. The shell wall (*c.* 2 μ thick) is irregularly studded with granules of varying shapes and sizes. The sutural crests are quite well defined, but low, and indicate a reflected tabulation of 3′, 1a, 6″, 6c, 6‴ (—7‴?), 1p., 1⁗. The crests, demarcating the three apical plates, extend along the apical horn and give rise to three small spines at its distal termination. Plates 2″, 3″ and 4″ are relatively large, plates 1″ and 5″ rather elongate and plate 6″ is reduced due to the anterior intercalary plate. In the postcingular series, plates 1‴ and 2‴ are reduced and plate 7‴ does not have a clearly marked plate boundary. Plate 2‴ possesses a curved line of ornamentation which is characteristic of *Cribroperidinium* Neale & Sarjeant. There is a single posterior intercalary plate and a large antapical plate.

The cingulum is strongly laevo-rotatory and varies considerably in width (2–5 μ), being constricted at the cingular plate boundaries and expanding on either side. The sulcus is broad and possesses a central depressed area of elongate shape. A archaeopyle is present.

FIGURED SPECIMEN. G.S.M. slide PF. 3987, specimen 2. Lower Chalk, H.M. Geological Survey Borehole, Fetcham Mill, Surrey at 730 feet depth, Upper Cretaceous (Cenomanian).

DIMENSIONS. Overall length 75 μ, overall width 65 μ, length of horn 14 μ.

REMARKS. The form of the apical horn, the type of granulation and the shape of the cingular plates distinguish this species from all described forms. The shape of the shell and the tabulation are most comparable to *G. exilicristata* suggesting a relationship between the two species.

Genus ***CRIBROPERIDINIUM*** Neale & Sarjeant emend.

Emended diagnosis. Proximate cysts, subspherical to ovoidal, thick-walled. Crests numerous and well developed. Tabulation ?6′, (1–5a), 8–9″, oc, 9‴, 1p, 1–3p.v. (5–7 p.c.), 0⁗ (—?2⁗). Cingulum laevo-rotatory. Archaeopyle precingular.

Type species. *Cribroperidinium sepimentum* Neale & Sarjeant 1962.

Remarks. The diagnosis has been emended to draw attention to the fact that the anterior intercalary series and the posterior circle series of plates are not always readily distinguishable. The tabulation attributed to this genus by Neale & Sarjeant was 6′, 1–5a, 8″, 9‴, 1p, 1–2p.v. 6–?7p.c., 0⁗. In determining the tabulation they numbered all the delimited areas on the shell surface in the normal manner. This numbering procedure has been used in the study of *C. intricatum* sp. nov. with certain reservations. Difficulties arose due to the large number of delimited areas and also to some variation on the dorsal surface of the hypotract. Some of the crests are rudimentary and others, although appearing fairly normal, are unusual in their position. It was discovered that by the removal of these unusual crests a normal *Gonyaulax*-type tabulation could be reconstructed. This is clearly shown in Figs. 11A, B, of the ventral surface of the holotype of *C. intricatum*. Thus *Cribroperidinium* is basically a form of *Gonyaulacysta* which possesses additional crests. These additional crests may correspond to an increase in the number of thecal plates composing the motile dinoflagellate, but this is thought to be unlikely since:

(a) the plates formed would be of an extremely unusual shape;

(b) these crests subdivide detached opercula demonstrably composed of a single precingular plate (3″);

(c) many of these crests are poorly developed and show considerable positional variation on the dorsal surface of the hypotract; and

(d) that by their removal a normal *Gonyaulax*-type tabulation remains. Thus, these additional crests may be regarded as an ornamentation or perhaps a rather, superficial cyst strengthening device. It is, therefore, considered more practical and correct to use a different numbering system for the *Cribroperidinium* cyst tabulation, *vis*, roman numerals.

Three species, *Gonyaulacysta orthoceras* (Eisenack), *G. muderongensis* (Cookson & Eisenack) and *G. edwardsi* (Cookson & Eisenack), are here transferred to *Cribroperidinium*. This genus appears to be very limited in stratigraphic range (Hauterivian—Lower Turonian) and, as such, is a useful stratigraphic indicator.

Cribroperidinium intricatum sp. nov.

(Pl. 2, figs. 1–3; Figs. 11, 12)

Derivation of name. Latin, *intricatus*, complicated—with reference to the complex crest arrangement.

Diagnosis. Shell subspherical, epitract and hypotract of similar size. Apical horn of moderate length, subconical. Shell wall moderately thick, granular and bears a few, randomly arranged tubercles. Crests usually in form of low ridges, well defined, sometimes membranous, delimiting a large number of plates on shell surface. Sutural spines absent. Plate II‴ crossed diagonally by low crest. Operculum possessing semi-circular crest. Sulcus possessing posterior ventral plates. Cingulum narrow, plates not defined.

Holotype. B.M. (N.H.). V. 51980 (1). Upper Lower Colorado, Fish Scale Zone, International Yarbo Borehole No. 17, Saskatchewan at 1,023 feet depth. Lower Cretaceous (Albian).

Dimensions. Holotype: overall length 120 μ, overall width 114 μ, length of horn 20 μ. Range: overall length 107 (125·1) 142 μ, overall width 101 (108·2) 126 μ. Number of specimens measured, 17.

Description. The shell wall is 1 to 1·5 μ in thickness and densely granular. The crests are typically low thickenings of the periphragm (2–3 μ wide), but in the antapical region, and occasionally elsewhere, the crests take the form of high flanges The latter (up to 6 μ in height) are membranous, thin and always perforate.

The number of apical plates always appears to be six. Plate I′, equivalent to the first apical plate, is elongate and abuts against the anterior end of the sulcus. The crest arrangement on the ventral surface appears to be practically constant and is characteristic of this species. The crests limiting the plates I′, I″, II″, III″, IV″, VII″ and VIII″ are always constant in position. Plates I‴ and II‴ are reduced due to the presence of a posterior intercalary plate. Plate II‴ always possesses a crest passing diagonally across it and the crest between plates III‴ and IV‴ is of a

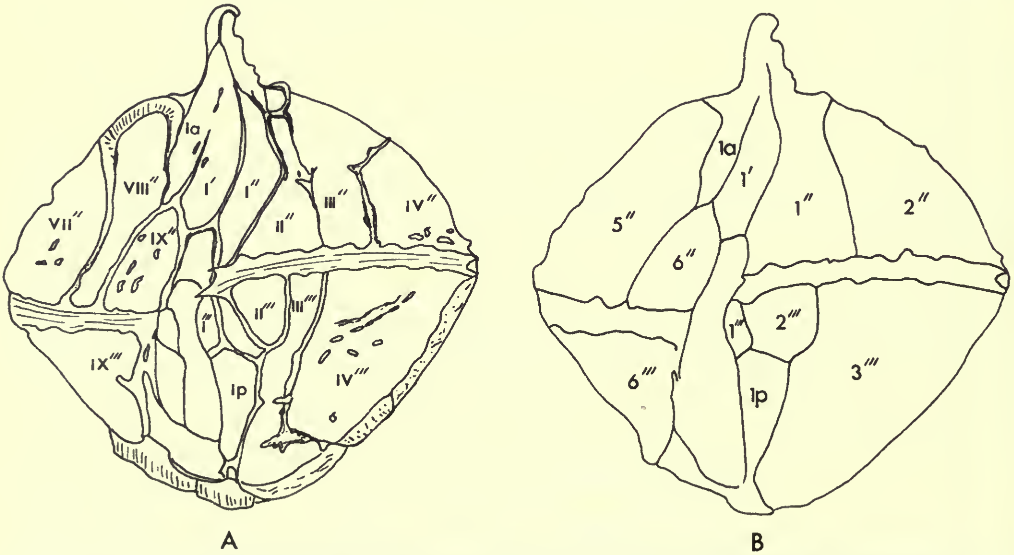

Fig. 11. *Cribroperidinium intricatum* sp. nov. A. Ventral surface of Holotype, (× 700). B. Reconstruction to show *Gonyaulax*-type tabulation (× 700).

characteristic right angle shape. The positions of the crests on the dorsal surface of the epitract are fairly constant, only varying in minor details. The large plate V″ is usually detached in archaeopyle formation and possesses a semi-circular crest from which radiate a small number of other crests (Pl. 2, fig. 3). These pass over the boundary of plate V″ to continue on adjacent parts of the epitract. The positions of the crests on the dorsal surface of the hypotract appear to be less constant in position. Their predominent direction is parallel to the longitudinal axis of the shell; sometimes a series of posterior circle plates may be present. Antapical plates, if present at all, are very reduced and obscured by the crestal membranes.

The cingulum is narrow (*c.* 6 μ in width), slightly laevo-rotatory, and tends to possess a thicker wall than is usual for the remainder of the shell. The sulcus only projects onto the epitract for a short distance, being considerably larger and wider on the hypotract. It is always divided into a number of posterior ventral plates by reduced crests.

Remarks. Figs 11B, 12B have been prepared from the holotype and one other specimen, omitting the additional crests, to show the basic *Gonyaulax*-type tabulation.

C. intricatum may be differentiated from *C. orthoceras* (Eisenack), *C. muderongensis* (Cookson & Eisenack), *Gonyaulacysta apionis* and *G. diaphanis* by its more spherical form, details of crest arrangement and the absence of spines. *C. edwardsi* (Cookson & Eisenack) is most similar, being almost spherical, but possesses a very well developed, stiff apical horn and the crests on the ventral surface are arranged differently. In particular the diagonal crest on plate II‴ is absent. *Gonyaulax* sp. (Górka 1963) from the Cenomanian of Poland is very similar and may be conspecific with *C. intricatum.*

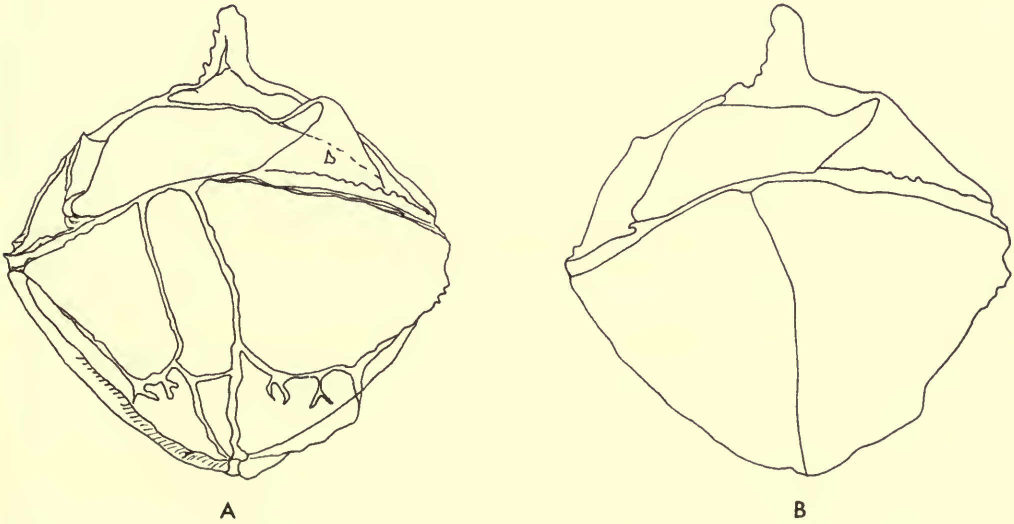

Fig. 12. *Cribroperidinium intricatum* sp. nov., A. Dorsal surface of Holotype with archaeopyle (× 700). B. Reconstruction to show *Gonyaulax*-type tabulation (× 700).

OCCURRENCE. *C. intricatum* is very rare in the British Cenomanian and has been observed only in samples FM 840, CB 1 and CB 7. At Escalles it is infrequent in sample E 201, very rare in sample E 195 and lacking elsewhere. In the Saskatchewan sample Sas 1023 it is common, in sample Sas 1084 rare and is lacking in all the other North American samples. It is interesting to record that this species was observed in the Albian sample FM 886 from Fetcham Mill. Thus *C. intricatum* has a range from Albian to Lower Cenomanian in the examined material.

OTHER SPECIES

The following species are here attributed to the genus *Cribroperidinium* on the basis of overal shape, and number and position of periphragm crests:—

Cribroperidinium orthoceras (Eisenack 1958) comb. nov., 1958 *Gonyaulax orthoceras* Eisenack, Neues. Jb. Geol. Paläont., Abh., **106** (3) 388: pls. 21, figs. 3–14; 24, fig. 1; text-figs. 2, 3.
Cribroperidinium edwardsi (Cookson & Eisenack 1958) comb. nov., 1958 *Gonyaulax edwardsi* Cookson & Eisenack: Proc. R. Soc. Vict., **70** (1), 32–33; Pl. III, figs. 5, 6, text-fig. 7.
Cribroperidinium muderongensis (Cookson & Eisenack 1958) comb. nov., 1958 *Gonyaulax muderongensis* Cookson & Eisenack: Proc. R. Soc. Vict., **70** (1), 32; Pl. III, figs. 3, 4, text-fig. 15.

Gonyaulacysta apionis (Cookson & Eisenack 1958) and *G. diaphanis* (Cookson & Eisenack 1958), both from the Lower Cretaceous of Australia, are of similar appearance to forms included in *Cribroperidinium* and may at a later date be transferred to this genus.

Eisenack (1958 text-figs. 2, 3) figured the ventral surface tabulation of *C. orthoceras* omitting, or dotting in, some of the crests which are seen to be present on the photographs of the same specimens. Thus a true representation of the crestal positions was not given, somewhat misleading later workers. These figures have been redrawn (Figs. 13A, B) from the photographs and show the remarkable similarity between the ventral surface of *C. orthoceras* and that of *C. intricatum*. For this reason the former species has been transferred to *Cribroperidinium* and the diagnosis emended. Eisenack does in fact compare and contrast his species with the reattributed Australian forms above, also with *Gonyaulactysa wetzeli* (Lejeune Carpentier 1939) and *G. obscura* (Lejeune-Carpentier 1946), all of which he considers to be in the same group. The latter two species, however, have a typical *Gonyaulacysta* tabulation and must remain in that genus.

Cribroperidinium orthoceras (Eisenack) emend.

(Figs. 13A, B)

1958 *Gonyaulax orthoceras* Eisenack : 388, pl. 21, figs. 3–14, pl. 24, fig. 1; text-figs. 2, 3.
1959 *Gonyaulax orthoceras* Eisenack; Gocht : 54, pl. 5, figs. 12, 13.
1961 *Gonyaulax orthoceras* Eisenack; Alberti : 6, pl. 11, figs. 1–3.
1963 *Gonyaulax orthoceras* Eisenack; Górka : 30, pl. 3, figs. 1–4.
1965 *Gonyaulax orthoceras* Eisenack; Balteş : 12, pl. 3, figs. 95–99.

EMENDED DIAGNOSIS. Shell ovoidal, moderately thick-walled, bearing strong, thorn-like apical horn constituting approximately one quarter of shell length. Shell wall granular bearing tubercles. Distinct tabulation marked by strong, low crests delimiting large number of plates. Plate II‴ crossed diagonally by low crest and operculum possessing semi-circular crest. Cingulum narrow, devoid of plate boundaries.

Holotype. The specimen illustrated by Eisenack (1958, pl. 21, fig. 5) from Preparation Ob. Apt. No. 32. Aptian glauconitic limestone, Deutschen Erdol A. G., Erdolwerke Holstein boring Marne, Feld Heide, North Germany, at 761·7 metres depth.

Remarks. The emended diagnosis excludes those forms described by Sarjeant (1966) from the Speeton Clay which are to be described elsewhere under a new specific name.

Genus ***CARPODINIUM*** Cookson & Eisenack, 1962

Carpodinium obliquicostatum Cookson & Hughes

(Pl. 1, figs. 3, 4)

1964 *Carpodinium obliquicostatum* Cookson & Hughes : 48, pl. 6, figs. 1–6.
1967 *Carpodinium obliquicostatum* Cookson & Hughes; Clarke & Verdier: 23, pl. 2, figs. 4, 5.

Description. The shell is elongate-ovoidal and bears relatively high sutural crests. The latter are smooth or slightly granular and the distal margin may be entire or spinous. The short apical horn is a prolongation of one of the larger crests and is typically asymmetrically placed. The periphragm of the shell possesses an unusual ornamentation—small areas of triangular to polygonal shape, composed of thick periphragm, are separated by narrow anastomosing " canals " where the periphragm is unthickened or perhaps absent (Pl. 1, fig. 4).

The cingulum is marked by indentations in some of the crests and is not apparent on the shell surface. The sulcus, delimited by crests, is occasionally observable and extends the length of the shell, being narrow near the apex and widening posteriorly. The precingular and postcingular plates, probably six in each series, are very elongate and difficult to discern because of the obscuring nature of the high crests. A precingular archaeopyle is commonly present. Four apical plates and a single antapical plate appear to be present. Intercalary plates were not observed.

Dimensions. Range of observed specimens: overall length 56(69·5) 82 μ, overall width 33(43·8) 57 μ, height of crests 6–15 μ. Number of specimens measured, 16.

Remarks. The Cenomanian specimens studied resemble the type material from the Upper Albian and Lower Cenomanian of Cambridgeshire in all respects.

Occurrence. *C. obliquicostatum* is a rare to very rare species found at all horizons throughout the Cenomanian of Fetcham Mill and Compton Bay and in three samples from Escalles (E 195, E 189 and E 159).

Genus ***ELLIPSODINIUM*** Clarke & Verdier 1967

Remarks. A number of microplankton genera have been described as possessing a reticulate shell wall, occasionally with an outer membrane but only rarely with any signs of tabulation. In all the described forms possessing a cingulum the archaeopyle is apical. Hence the combination of numerous crests, a cingulum and a precingular archaeopyle differentiates *Ellipsodinium* from all previously described genera.

Ellipsodinium rugulosum Clarke & Verdier

(Pl. 3. fig. 1; Figs. 14C, D)

1967 *Ellipsodinium rugulosum* Clarke & Verdier: 69, pl. 14, figs. 4–6, text-fig. 29.

Dimensions. Range of observed specimens: shell length 30 (37.7) 46 μ, shell width 25 (33·6) 40 μ, maximum height of crests 1·5 (2·4) 3·5 μ. Number of specimens measured, 20.

Description. The crests are thin, occasionally perforate lamellar structures which thicken slightly before joining the shell surface. The cingulum may be delimited by a pair of crests, or in the absence of cingular crests, crests may terminate abruptly at its borders. Rarely crests traverse the cingulum. The sulcus is not obvious because of the nature of the elongate areas outlined by the crests. Apical and antapical processes or horns are absent. The precingular archaeopyle is subtriangular in outline.

Occurrence. *E. rugulosum* is a rare to fairly common species at all horizons throughout the Cenomanian of Fetcham Mill, Compton Bay and Escalles. It was not observed in the North American material.

Cyst-Family **PAREODINIACEAE** Gocht emend. Sarjeant & Downie 1966

Genus ***APTEODINIUM*** Eisenack 1958

Remarks. Members of this genus have occasionally been observed in the European Cenomanian and have been placed in *A. granulatum*. Rarely plate boundaries may be discernable. This fact together with the overall shape and the well developed precingular archaeopyle indicate that this genus is closely related to *Gonyaulacysta* and at a future date may be transferred to the Cyst-Family *Gonyaulacystaceae*.

Apteodinium granulatum Eisenack

(Pl. 3, figs. 5, 6)

?1935 *Palaeoperidinium ventriosum* O. Wetzel; Deflandre : 228, pl. 5, fig. 5; pl. 6, figs. 9, 10.
?1936*b* *Palaeoperidinium ventriosum* O. Wetzel; Deflandre : 27, pl. 5, figs. 1–4.
?1936*a* *Palaeoperidinium ventriosum* O. Wetzel; Deflandre: fig. 100.
1958 *Apteodinium granulatum* Eisenack : 386, pl. 23, figs. 8–14, text-fig. 1.
1958 *Apteodinium granulatum* Eisenack; Gocht : 64, pl. 5, fig. 2.
1961 *Apteodinium granulatum* Eisenack; Alberti : 24, pl. 4, figs. 4–6.
1963 *Apteodinium granulatum* Eisenack; Balteş : 584, pl. 4, fig. 11.

Description. Shell subspherical with a moderately thick wall (1–2·5 μ) and possessing a stout conical horn. The wall is densely granular, the granules often being elongated into fine, short processes which are linked laterally thus covering the shell surface with an intricate network of a matted furry appearance. The cingular boundaries are always visible as slight thickenings of the periphragm. Very rarely similar but more reduced thickenings indicate the presence of plate boundaries. A precingular archaeopyle is commonly developed.

DIMENSIONS. Range of observed specimens: overall length 42 (48·2) 53 μ, width 31 (38·6) 44 μ, length of apical horn 5 (6·1) 8 μ. Number of specimens measured, 9.

REMARKS. The Cenomanian specimens are very similar in appearance to the type material described by Eisenack from the Aptian of Germany. The matted, furry appearance was not described but when this feature is only slightly developed the shell wall merely appears to be very granular. The Aptian and Cenomanian examples of *A. granulatum* appear to be comparable to *Palaeoperidinium ventriosum* O. Wetzel as illustrated by Deflandre (1935, 1936*a*, *b*). The holotype of this species has been re-examined by Lejeune-Carpentier (1946) and a distinct tabulation described. Deflandres' forms which do not possess a tabulation are hence here tentatively reattributed to *A. granulatum*.

OCCURRENCE. Only two specimens have been recorded from the English Cenomanian, both from sample FM 690. At Escalles two specimens have been recorded from both samples E 183 and E 153, and three from sample E 165. *A. granulatum* is fairly common in sample FM 886 (Albian) from Fetcham Mill but is absent in the North American material and from sample FM 520 (Turonian).

Genus ***TRICHODINIUM*** Eisenack & Cookson emend. Clarke & Verdier

REMARKS. This genus differs from *Exochosphaeridium* Davey, Downie, Sarjeant & Williams (1966) by the presence of a well developed cingulum and by the shorter spines.

Trichodinium castaneum (Deflandre)

Pl. 11, figs. 1–3

1935 *Palaeoperidinium castanea* Deflandre : 49, pl. 6, fig. 8.
1936*b* *Palaeoperidinium castanea* Deflandre; Deflandre : 25, pl. 16, figs. 1–4.
1936*a* *Palaeoperidinium castanea* Deflandre; Deflandre: fig. 99.
1952*b* *Palaeoperidinium castanea* Deflandre; Deflandre: fig. 96.
1962*b* *Palaeoperidinium castanea* Deflandre; Cookson & Eisenack : 489, pl. 3, figs. 9–11.
1964 *Palaeoperidinium castanea* Deflandre; Cookson & Hughes : 49, pl. 5, fig. 14.
1967 *Trichodium castanea* (Deflandre) Clarke & Verdier: 19, pl. 1, figs. 1, 2.

DESCRIPTION. The shell is subspherical with occasionally a small apical horn or a tuft of apical spines. The shell wall is slightly punctate and bears numerous small spines. These are solid, often bifurcate either proximally or distally, and typically terminate in a small bifurcation. Rarely they may be acuminate. The cingulum (3–5 μ in width) is marked by two parallel lines of thickening along which spines are concentrated. Lines of similar thickening sometimes occur perpendicularly to the cingulum and are probably sutural. A sulcus has not been observed. A precingular archaeopyle is commonly present.

DIMENSIONS. Range of observed specimens: shell diameter 35 (49·0) 64 μ, length of spines 1 (3·3) 5 μ. Number of specimens measured, 16.

REMARKS. The Cenomanian specimens resemble the type material from the Upper Cretaceous of France in all respects. The presence of a precingular archaeopyle, an apical prominence or apical spines, and a well developed cingulum indicate that this species should be placed in *Trichodinium*. *T. intermedium* Eisenack & Cookson, from the Aptian to Lower Albian of Australia, is very similar but is larger (shell diameter 69–90 μ).

OCCURRENCE. *T. castaneum* is a rare species occurring at most horizons throughout the Cenomanian of Fetcham Mill, Compton Bay and Escalles. It has not been recorded from the North American samples. This species has a recorded stratigraphic range from the Aptian to the Senonian (Deflandre).

Cyst-Family **MICRODINIACEAE** Eisenack emend. Sarjeant & Downie 1966

Genus ***MICRODINIUM*** Cookson & Eisenack emend. Sarjeant 1966

REMARKS. *Microdinium* differs from *Gonyaulacysta* primarily in possessing a single apical plate which is detached in archaeopyle formation. Górka (1965), in describing Upper Jurassic assemblages, erected the genus *Tetrasphaera* which is diagnosed as having a feebly marked tabulation and short spines on the plate boundaries. Górka has since stated (personal communication with Dr. W. A. S. Sarjeant) that this genus differs from *Microdinium* only in these two respects. However, it follows that if the tabulation is not clear it is difficult to compare this new genus with *Microdinium* or any other genus possessing a tabulate cyst, since the diagnosis of these genera is primarily based on the observed tabulation. Also, spines have been observed on the plate boundaries of *Microdinium*, even in the type species. Thus it would appear that *Tetrasphaera* at the moment is not precisely defined.

Microdinium cf. ***ornatum*** Cookson & Eisenack.

(Pl. 4, fig. 5; Figs. 13C, F)

1966*a* *Microdinium* cf. *ornatum* Cookson & Eisenack; Sarjeant : 149, pl. 16, figs. 3–6, text-fig. 38.
1967 *Microdinium ornatum* Cookson & Eisenack; Clarke & Verdier: 66, pl. 5, figs. 11–14.

DESCRIPTION. The shell is subspherical to ovoidal possessing a smooth body wall ornamented by a few large tubercles. The latter may be flat or distinctly concave distally. In two specimens small tubercles were seen to delimit a plate in the posterior portion of the ventral area. The plates are bordered by short, broad projections (Fig. 13F), which may be isolated or united distally.

DIMENSIONS. Range of observed specimens: shell length 31–34 μ, width 23–31 μ, height of crests 1–2 μ. Number of specimens measured, 6.

REMARKS. *M.* cf. *ornatum* differs from *M. ornatum* Cookson & Eisenack (1960*a*) in that (i) the small cingular plate, ventral to plate 6c, is absent or has a very reduced ventral suture, and (ii) the plates are not bordered by ledges, which are sometimes perforate, but by isolated tubercles and spines.

OCCURRENCE. *M.* cf. *ornatum* is a rare species in the material examined being found only in the following samples: FM 810, FM 670, FM 650, FM 520 (Turonian), E 189 and E 153. In Australia *M. ornatum* has a stratigraphic range from the Albian to the Lower Turonian.

Microdinium setosum Sarjeant.

(Pl. 2, fig. 4; Fig. 13H)

1966 *Microdinium setosum* Sarjeant : 151, pl. 16, figs. 9, 10; text-fig. 39.
1967 *Microdinium echinatum* Clarke & Verdier: 64, pl. 1, figs. 9, 10, text-fig. 26.

DESCRIPTION. The shell is spherical to ovoidal and possesses a well developed tabulation. The shell surface is either lightly or coarsely granular. The two plates observed by Sarjeant in the medial region of the sulcus are not always delimited. The sutural crests are often relatively high and give rise to numerous, well developed thorn-like spines (Fig. 13H).

DIMENSIONS. Range of type material: shell length 25 (29·3) 37 μ, width 21 (26·2) 31 μ, maximum height of crests 1·5 (3·8) 7 μ. Number of specimens measured, 22.

REMARKS. In general form *M. setosum* is similar to *M. ornatum* but differs in the presence of spiny crests, a dense granulation and, slightly, in the tabulation exhibited.

OCCURRENCE. *M. setosum* is an infrequent to fairly common species at most horizons throughout the Cenomanian of Fetcham Mill, Compton Bay and Escalles. It has also been recorded from the Albian of Fetcham Mill.

Microdinium distinctum sp. nov.

(Pl. 2, figs. 9–11; Figs. 13D, E. I)

1967 *Microdinium ornatum* Cookson & Eisenack; Clarke & Verdier: pl. 5, figs. 11–12.

DERIVATION OF NAME. Latin, *distinctus*, different—with reference to the distinctive appearance of this species.

DIAGNOSIS. Shell subspherical, thick-walled, smooth. Sutural crests well developed bearing short, broad, flat-topped spines. Reflected tabulation 1, 0a, 6″ 6‴, 1p, 1⁗; plates 1″ and 6″ very reduced and cingular plates absent. Cingulum broad, weakly laevo-rotatory.

HOLOTYPE. G.S.M., slide PF 3989, (1). Lower Chalk, H.M. Geological Survey Borehole, Fetcham Mill, Surrey at 730 ft. depth. Upper Cretaceous (Cenomanian).

DIMENSIONS. Holotype: shell length 36 μ, width 37 μ, height of crests *c.* 2 μ. Range: shell length 29–36 μ, width 30–37 μ, height of crests 2–2·5 μ. Number of specimens measured, 7.

DESCRIPTION. The shell wall is relatively thick, *c.* 1 μ, and develops pronounced ridges at the plate boundaries. The sutural spines are closely set, very broad and flat distally.

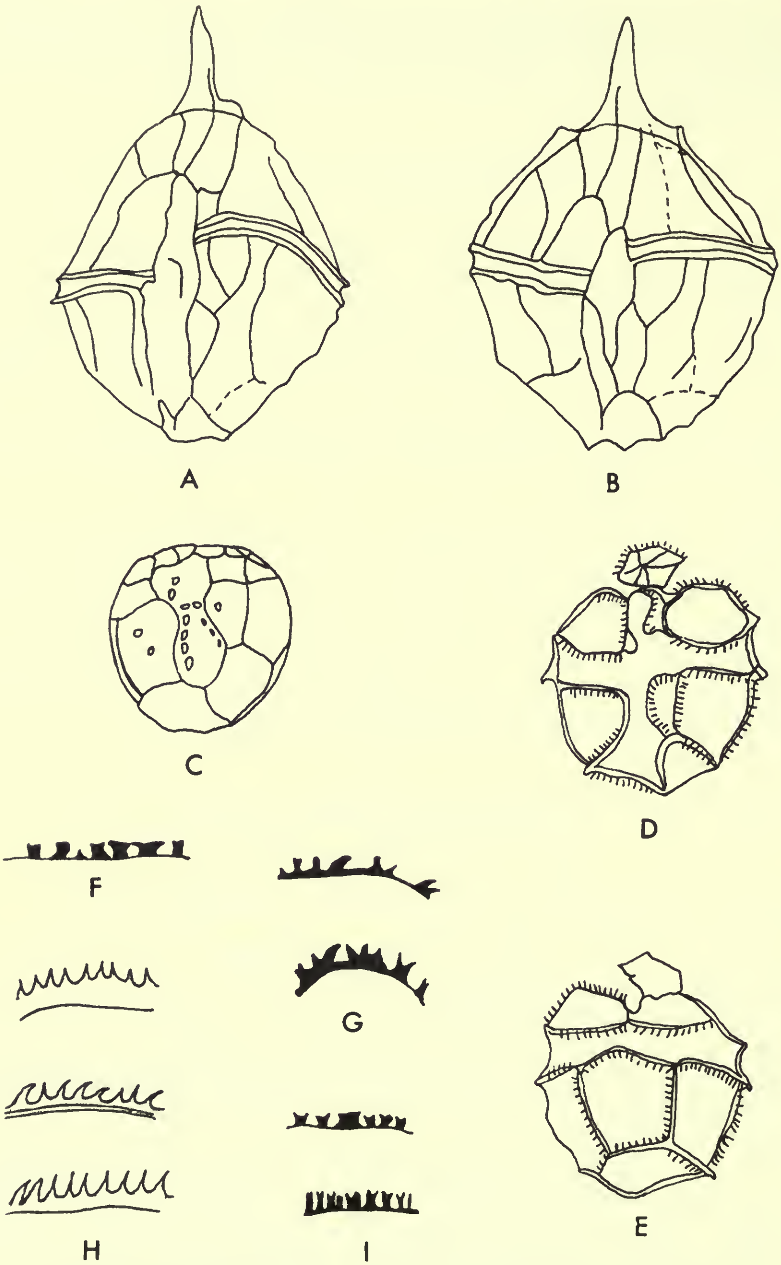

FIG. 13. *Cribroperidinium orthoceras* (Eisenack). A. Specimen illustrated by Eisenack (1958, text-fig. 3) redrawn to show full crestal arrangement. B. Holotype (Eisenack 1958, text-fig. 2) redrawn to show full crestal arrangement. *Microdinium* cf. *ornatum* Cookson & Eisenack, C. Ventral surface of Holotype (× 700). *Microdinium distinctum* sp. nov., D. Ventral surface of Holotype (× 700), E. Dorsal surface of Holotype (× 700). *Microdinium* cf. *ornatum* Cookson & Eisenack, F. Sutural spines. *Microdinium variospinum* sp. nov., G. Sutural spines. *Microdinium setosum* Sarjeant, H. Sutural spines. *Microdinium distinctum* sp. nov., I. Sutural spines.

The precingular plates are generally smaller than the postcingular plates. Plates 1″ and 6″ are small and appear as slight projections in the ventral area. This is widest posteriorly and is open anteriorly. The apical plate is six-sided and is lost in archaeopyle formation. The archaeopyle possesses slits extending posteriorly between the precingular plates.

REMARKS. *M. distinctum* may be distinguished from all other species of *Microdinium* by the thick, smooth shell wall, the form of the precingular plates and the absence of cingular plates. It is considered that the absence of the latter does not, at present, warrant the erection of a new genus.

OCCURRENCE. This species is very rare, being recorded only seven times, from the following samples: FM 790, FM 730, FM 710, FM 690, E 153 and CB 17. It has never been observed in the lower horizons of the Cenomanian.

Microdinium variospinum sp. nov.

(Pl. 2, figs. 5, 6; Fig. 13G)

DERIVATION OF NAME. Latin, *varius*, different; *spinosus*, spine—with reference to the variable appearance of the spines.

DIAGNOSIS. Shell subspherical to ovoidal; shell wall thin, smooth, granular or lightly reticulate. Sutural crests low, bearing small number of variably shaped spines. These may be simple tubercles to complex bifurcating protrusions. Reflected tabulation 1′, 0a, 6″, (6c), 6‴, 1p, 1⁗; cingular plate boundaries very faint or absent. Cingulum weakly laevo-rotatory.

HOLOTYPE. B.M. (N.H.) V. 51981 (1). Lower Chalk, Bureau de Recherches Géologiques et Minières Borehole, Escalles, Pas de Calais at 165 metres depth. Upper Cretaceous (Cenomanian).

DIMENSIONS. Holotype: shell length 24 μ, width 23 μ, length of spines 1–1·5 μ Range: shell length 20 (23·6) 27 μ, width 17 (20·0) 23 μ, length of spines 1–3 μ. Number of specimens measured, 9.

DESCRIPTION. The cingular plate boundaries are usually absent, however, one Saskatchewan specimen had them lightly defined. The sutural spines are few in number and tend to be concentrated at the posterior of the shell (Pl. 2, fig. 5). They are stout and may be either pointed or flattened distally (Fig. 13G).

REMARKS. The characteristic features of *M. variospinum* are the nature of the shell wall, the form of the spines and the lack of well defined cingular plate boundaries. These characters together differentiate this species from all other described species.

OCCURRENCE. *M. variospinum* is a rare species found at all horizons, save the lower three, at Escalles, and in sample CB 1, CB 7 and Sas 1084. It has not been recorded from Fetcham Mill.

Microdinium veligerum (Deflandre) comb. nov.

(Pl. 3, fig. 4; Pl. 4, fig. 4)

1937 *Micrhystridium veligerum* Deflandre : 81, pl. 12, fig. 9.
1943 *Ceratocorys veligera* (Deflandre) Lejeune–Carpentier : 22, text-figs. 1–6.
1952*a* *Ceratocorys veligera* (Deflandre) Deflandre : 120, text-fig. 102.
1952b *Ceratocorys veligera* (Deflandre) Deflandre: text-figs. 304 A–C.
1967 *Eisenackia crassitabulata* Deflandre & Cookson; Clarke & Verdier: 64, pl. 8, figs. 4–6.

DESCRIPTION. The shell is ovoidal, densely granular and bears a number of high crests delimiting a tabulation. The crests are distinctive, being 1 to 5 μ in height, with typically a smooth outer margin. They consist of two membranes, joined distally and diverging proximally to form a broad base, 1 to 3 μ, wide to the crest. There is between the two membranes a crestal cavity which is occasionally subdivided by septa, particularly where two crests diverge. Here a conical chamber is usually found. The reflected tabulation appears to be 1', ?5'', 6c, 6''', 1p, 1''''. The hypotract is considerably larger than the epitract, the latter being devoid of crests and usually possessing a pentagonal apical archaeopyle. The shape of the latter is the only indication that there are five precingular plates. The cingulum is broad and does not appear to be spiral. Plate 1''', and to a lesser extent 2''', are reduced to accommodate the posterior intercalary plate. The remaining four postcingular plates are large and there is a single large antapical plate. The sulcus is very narrow just posterior to the cingulum and then widens rapidly towards the antapex. The sulcus extends onto the epitract where it sometimes bears five small sulcal plates.

DIMENSIONS. Range of observed specimens: shell length 28 (31·5) 38 μ, width 25 (28·2) 32 μ. Number of specimens measured, 13.

REMARKS. Lejeune-Carpentier (1943) placed this species, originally observed in the Upper Cretaceous of France, in the genus *Ceratocorys* Stein (1883) on the basis of its similarity to motile dinoflagellates contained in this genus. However, it is a cyst possessing an apical archaeopyle and should not be attributed to a motile dinoflagellate genus. Thus this species is here transferred to *Microdinium* on the basis of the tabulation, apical archaeopyle, reduced size of epitract compared with the hypotract and overall small size. *M. veligerum* does, however, differ slightly from the other species in this genus by the apparent absence of crests on the epitract and the probable presence of five precingular plates instead of six.

Eisenackia crassitabulata as illustrated by Clarke & Verdier (1967) is undoubtedly *M. veligerum*. The former, as originally described from the Australian Lower Tertiary, is of different overall form and is considerably larger (72–78 by 55–67 μ). The size of the specimen illustrated by Clarke & Verdier is approximately 30 by 32 μ and is thus comparable to the Cenomanian specimens of *M. veligerum*. *E. crassitabulata* has been recorded from the Lower Tertiary and also from the Maestrichtian of South Africa by the present author. *M. irregulare* Clarke & Verdier (1967) appears to be very similar to *M. veligerum* and any definite distinction is not apparent.

OCCURRENCE. The Cenomanian forms examined resemble the specimens illustrated by Lejeune-Carpentier in all respects. *M. veligerum* is an infrequent to common species at all horizons, save two, at Fetcham Mill, Compton Bay and Escalles. These two horizons are basal Cenomanian, FM 840 and CB 1, and it was not recorded by Cookson & Hughes (1964) from the Upper Albian/basal Cenomanian of Cambridgeshire. It is also absent in the North American material and has not been described from Australia. This species is present in sample FM 520 of Turonian age. *M. veligerum* thus appears for the first time just above the base of the Cenomanian and extends into the Turonian but is, apparently, of restricted geographical distribution.

?***Microdinium crinitum*** sp. nov.

(Pl. 2, figs. 7, 8)

1967 *Cometodinium obscurum* Deflandre & Courteville; Clarke & Verdier: pl. 10, fig. 3: pl. 11, fig. 9.

DERIVATION OF NAME. Latin, *crinitus*, hairy—with reference to the numerous hair-like spines.

DIAGNOSIS. Shell subspherical, periphragm granular and giving rise to numerous, fine, flexuous spines. Sutural crests low, bearing numerous spines. Cingulum wide, composed of elongate plates. Epitract smaller than hypotract. Archaeopyle not normally visible.

HOLOTYPE. G.S.M. slide PF 3990(1). Lower Chalk, H.M. Geological Survey Borehole, Fetcham Mill, Surrey at 690 feet depth. Upper Cretaceous (Cenomanian.)

DIMENSIONS. Holotype: shell diameter 27 by 28 μ, length of spines *c.* 12 μ. Range: shell diameter 24 (30·1) 38 μ, length of spines 6–19 μ. Number of specimens measured, 18.

DESCRIPTION. The periphragm granules, which are evenly spaced on the shell surface, are up to 0·5 μ high, and often form the bases of the hair-like spines. The latter tend to be especially concentrated along the sutures, and because of this tendency and the spherical form of the shell, it has not been possible to fully formulate a tabulation. However, precingular, cingular and postcingular plates are quite obvious when the orientation is favourable, the precingular plates being smaller than the postcingular plates. The cingulum is broad, *c.* 5 μ. The archaeopyle, although it has not been observed, is probably apical.

REMARKS. The numerous hair-like spines and the tabulation easily distinguish ?*M. crinitum* sp. nov. from all previously described forms of dinoflagellate cysts. The overall shape, the small size and the fact that the epitract is smaller than the hypotract all indicate that this species is closely related to the genus *Microdinium*. However, plate spines have not been recorded in *Microdinium*, although a granulation has, and since the tabulation has not been elucidated in the present species it is only placed tentatively in this genus.

OCCURRENCE. ?*M. crinitum* is infrequent at all horizons throughout the Cenomanian of Fetcham Mill, Compton Bay and Escalles and is also present in the Albian sample from Fetcham Mill, sample FM 886. It has only once been recorded at Saskatchewan, in sample Sas 835 (Cenomanian).

Genus ***HISTIOCYSTA*** nov.

Derivation of name. Greek, *histos*, mesh or network; *kystis*, sac or cell—with reference to the reticulate ornamentation on the shell surface.

Diagnosis. Proximate cysts, spherical to subspherical; shell wall composed of two layers; outer layer giving rise to low crests. Crests reflecting *Gonyaulax*—type tabulation and coarse, subsidiary reticulation within plate boundaries. Sutural crests better defined than crests of subsidiary reticulation. Archaeopyle apical with angular margin. Operculum probably single apical plate.

Type species. *Histiocysta palla* sp. nov. Lower Chalk (Cenomanian); England.

Remarks. The reasonably well defined tabulation, the plate ornamentation and the apical archaeopyle easily distinguish *Histiocysta* from all previously described genera. The most similar genera are *Ellipsoidictyum* Klement (1960*b*) and *Dictyopyxidia* Eisenack (1961), both from the Upper Jurassic. Both genera possess an apical archaeopyle and a cingulum but a distinct *Gonyaulax*-type tabulation is absent. However, it seems probable that *Histiocysta* is genetically related to these two genera. Although the precise tabulation of *Histiocysta* cannot be elucidated the presence of precingular, cingular and postcingular series of plates together with an apical archaeopyle indicate that this genus belongs to the Family Microdiniaceae.

Histiocysta palla sp. nov.

(Pl. 1, figs. 5, 6; Figs. 14A, B)

1939 *Micrhystridium* sp.? Deflandre & Courteville : pl. 3, fig. 4.

Derivation of name. Greek, *palla*, ball—with reference to the more or less spherical shape of this species.

Diagnosis. Shell spherical to subspherical, thin-walled, periphragm smooth and forming a reticulate network of crests. Network consisting of reflected dinoflagellate tabulation with central region of each plate occupied by coarse but simple reticulation.

Holotype. G.S.M. slide PF 3052 (2). Lower Chalk, H.M. Geological Survey Borehole, Fetcham Mill, Surrey at 650 feet depth. Upper Cretaceous (Cenomanian).

Paratype. G.S.M. slide PF 3991(1). Lower Chalk, H.M. Geological Survey Borehole, Fetcham Mill, Surrey at 710 feet depth. Upper Cretaceous (Cenomanian).

Dimensions. Holotype: shell diameter 30 by 33 μ, height of crests 4–5 μ. Paratype: shell diameter 26 by 29 μ, height of crests *c.* 2·5 μ. Range: shell diameter 25 (31·8) 38 μ, height of crests 1–5 μ. Number of specimens measured, 19.

Description. The precingular and postcingular plates may be observed on most specimens but the exact tabulation has not, as yet, been elucidated. The central region of each plate is occupied by a coarse, subpolygonal reticulation which occasionally extends to the plate boundaries (Figs. 14A, B). The cingular region is clearly defined by crests and encircles the shell. Cingular plates are not usually discernible, the entire region being occupied by a coarse reticulation. An apical archaeopyle with an angular margin is typically present, the six-sided operculum often remaining attached to the shell.

REMARKS. The combination of apical archaeopyle, tabulation and reticulation makes *H. palla* an easily recognizable species distinct from all previously described

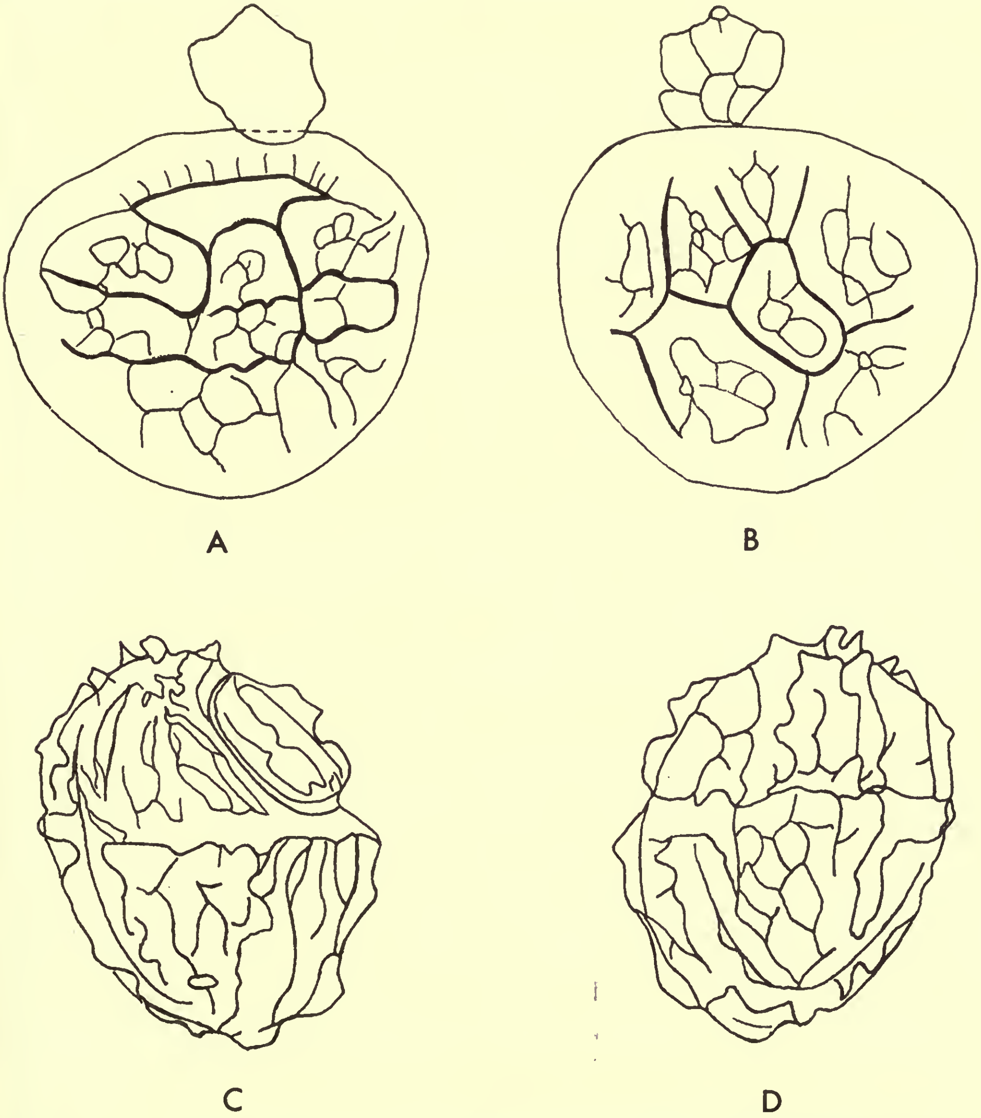

FIG. 14. *Histiocysta palla* sp. nov., A. Lateral view of Holotype showing attached operculum, apical archaeopyle, precingular plates and cingulum (× 1300). B. Lateral view of Holotype showing well defined plate boundaries (× 1300). *Ellipsodinium rugulosum* Clarke & Verdier, C. Lateral view showing partially detached operculum and cingulum (× 1300). D. Lateral view (× 1300).

forms. This species was figured, but not described, by Deflandre & Courteville (1939) as *Micrhystridium* sp.? from the Senonian. *Membranilarnax* cf. *pterospermoides* Deflandre (1937) is of similar form but does not possess a reticulation.

Occurrence. *H. palla* is found throughout the European Cenomanian, except for the lowermost horizons. It is fairly common at Fetcham Mill but rare at Compton Bay and Escalles. It has not been observed in the North American samples.

Cyst-Family **FROMEACEAE** Sarjeant & Downie 1966

Genus ***FROMEA*** Cookson & Eisenack 1958

Remarks. A number of specimens referable to the type species, *F. amphora*, do not appear to possess a cingulum. The absence of a cingulum makes this genus similar to *Chytroeisphaeridia* Sarjeant (1962). They differ, however, in that the archaeopyle of *Fromea* has a rounded margin, and in the elongate shape typical of the latter genus.

Fromea amphora Cookson & Eisenack

(Pl. 3, figs. 2, 3)

1958 *Fromea amphora* Cookson & Eisenack : 56, pl. 5, figs. 10, 11.

1966*b* *Fromea amphora* Cookson & Eisenack; Sarjeant : 209, pl. 22, fig. 4; pl. 23, fig. 3 (see also for earlier references).

Description. The shell is ovoidal, thick-walled (2–3 μ) and typically possesses an apical archaeopyle with a rounded margin. In one specimen (Pl. 3, fig. 3) the apical region is still attached and may be seen to be perfectly rounded. A cingulum was not observed in any of the specimens.

Dimensions. Range of observed specimens: shell length 56 (72·5) 85 μ, width 47 (60) 71 μ. Number of specimens measured, 6.

Remarks. The Cenomanian specimens are identical with the type material from the Aptian-Cenomanian of Australia except that the cingulum is absent. Cookson & Eisenack (1958) state, however, that the cingulum may be rather faint and it is probable that the European forms fall within the range of variation for this species. *F. amphora* has been recorded from the Barremian of England by Sarjeant (1966*b*). The specimens described by Sarjeant, like the Cenomanian forms, do not possess a cingulum. Maliavkina *et al.* (1961) describes some very similar, but rather smaller, forms from the Maestrichtian of Siberia, calling them *Chrysomonadinae*?. These forms possess the typical rounded archaeopyle of this genus.

Occurrence. Five specimens have been recorded from Fetcham Mill, from samples FM 810, 770, 750 and 650, and one specimen from Escalles, sample E 177.

Genus ***CHYTROEISPHAERIDIA*** Sarjeant 1962

Remarks. *Chytroeisphaeridia* and *Canningia* Cookson & Eisenack (1960*b*) are similar and probably fairly closely related. The latter is usually more polygonal, has an apical horn, and sometimes the vestiges of a cingulum.

Chytroeisphaeridia euteiches sp. nov.

(Pl. 3, figs. 8, 9)

Derivation of name. Greek, *euteiches*, well-walled—with reference to the stout wall of this species.

Diagnosis. Shell subspherical; shell wall thick and densely granular. Angular apical archaeopyle typically present.

Holotype. B.M. (N.H.) V. 51982 (2). Lower Chalk, Bureau de Recherches Géologiques et Minières Borehole, Escalles, Pas de Calais, at 159 metres depth. Upper Cretaceous (Cenomanian).

Dimensions. Holotype: shell length 53 μ, width 59 μ. Range: shell length 48–60 μ, width 49–59 μ. Number of specimens measured, 6.

Description. The shell wall is thick (2–3 μ) and may be composed of two layers. If the wall is bipartite then the inner layer is thin, the outer layer making up almost the entire wall thickness. This layer appears to be composed of minute cellular elements and is densely granular on the surface. The apical archaeopyle, when developed, is angular with small slits passing posteriorly from its margin between each precingular plate. A sulcal notch is also present (Pl. 3, fig. 8). Plate boundaries and cingulum are not discernible.

Remarks. This species is a simple, subspherical shell possessing an apical archaeopyle. One species, *C. chytroeides* Sarjeant (1962), from the Upper Jurassic of England, differs from C. *euteiches* in having a fairly thin and only slightly granular shell wall. *Chytroeisphaeridia* sp. Sarjeant (1965*b*) is similar in size and also granular but does not possess a thick shell wall. *Canningia rotundata* Cookson & Eisenack (1961) is also similar but tends to have a polygonal shell with a small apical horn.

Occurrence. *C. euteiches* has been recorded from two horizons only, E 165, & E 159 from Escalles, where it is infrequent.

Genus ***CASSICULOSPHAERIDIA*** nov.

Derivation of name. Latin, *cassiculus*, hunting-net; *sphaera*, ball—with reference to the surface reticulation of the shell.

Diagnosis. Proximate cysts; shell spherical to subspherical, composed of two layers, without apical or antapical protuberances. Periphragm giving rise to low crests or membranes which form a reticulate pattern. Tabulation absent. Archaeopyle apical with angular margin.

Type Species. *Cassiculosphaeridia reticulata* sp. nov. Lower Chalk (Cenomanian); France.

Remarks. The surface reticulation of this genus is very similar to that of *Ellipsoidictyum cinctum* Klement (1960). Both possess an apical archaeopyle, but whereas in *Cassiculosphaeridia* all signs of a tabulation are absent, in *Ellipsoidictyum* there is an obvious cingulum. *Dictyopyxidia* Eisenack (1961) is also very similar but possesses a cingulum and sulcus.

Cassiculosphaeridia reticulata sp. nov.

(Pl. 3, fig. 7; Pl. 4, fig. 3)

Derivation of name. Latin, *reticulatus*, net-like—with reference to the reticulate pattern formed by the periphragm crests.

Diagnosis. Shell spherical to subspherical. Shell surface bearing low ridges, forming a coarse reticulation, from which arise fine membranous crests. Shell wall lightly to densely granular.

Holotype. B.M. (N.H.) V.51981 (4). Lower Chalk, Bureau de Recherches Géologiques et Minières Borehole, Escalles, Pas de Calais, at 165 metres depth. Upper Cretaceous (Cenomanian).

Dimensions. Holotype: shell diameter 38 by 38 μ, height of crests 4 to 6 μ. Range: shell diameter 33 (43·6) 55 μ, maximum height of crests 3 (7·3) 11 μ. Number of specimens measured, 15.

Description. The areas delimited by the low ridges are typically subpolygonal but may be of irregular shape. They vary considerably in size, from 2 to 10 μ in diameter. The membranous crests are very fine and tend to be flexuous since supporting structures are absent.

Remarks. The surface reticulation, the absence of any tabulation and the apical archaeopyle together distinguished this species from all previously described forms.

Occurrence. *C. reticulata* is rare to common in samples from the Middle and Upper Cenomanian of Fetcham Mill (not found below sample FM 750), and from the Lower, Middle and Upper Cenomanian of Escalles (not found below sample E 207). This species was absent from the samples from Compton Bay and from North America.

Genus ***EPELIDOSPHAERIDIA*** nov.

Derivation of name. Greek, *epelidos*, cover or lid; *sphaera*, ball—with reference to the conical apical operculum which sometimes remains attached to the shell.

Diagnosis. Shell subpolygonal; epitract conical with small apical protuberance, hypotract polygonal with small antapical horn on one side. Shell wall two layered, periphragm giving rise to a moderate number of spines, truncated or forked distally Cingulum and sulcus outlined by spines. Cingulum slightly laevo-rotatory. Apical archaeopyle.

Type species. *Palaeoperidinium spinosum* Cookson & Hughes 1964. Cambridge Greensand (Cenomanian), England.

Remarks. The presence of an apical archaeopyle, together with a well developed cingulum and sulcus differentiate *Epelidosphaeridia* from all previously described genera. *Doidyx* Sarjeant (1966*b*) is most similar but differs in that the shell is asymmetrical, the hypotract is conical and a sulcus is absent.

Epelidosphaeridia spinosa (Cookson & Hughes) comb. nov.

(Pl. 3, figs. 10–12)

1964 *Palaeoperidinium spinosum* Cookson & Hughes : 49, pl. 8, figs. 6–8.
1967 *Palaeoperidinium spinosum* Cookson & Hughes: Clarke & Verdier: 70, pl. 14, figs. 10–12.

DESCRIPTION. The shell possesses convex sides, conical epitract and a hypotract which is more or less truncated posteriorly. A small apical prominence is commonly present. The periphragm is smooth or lightly granular and forms a moderate number of small, stout spines. The spines appear to be hollow, closed proximally, parallel sided, and are oblate distally or terminate with a small fork. The spines widen slightly before joining the shell and they are sometimes joined proximally. This is particularly well developed in the antapical region where the processes are joined medially and form a slight projection on one side of the shell. The cingulum is clearly delimited by two parallel lines of closely set spines and is 5 to 8 μ in width. It is only slightly helicoid and bears few spines on its surface. The sulcus in most specimens is clearly defined, being slightly hollowed and almost devoid of spines. The spines on the remainder of the shell surface are usually randomly arranged, but occasionally a vague alignment is present suggesting a tabulation. An apical archaeopyle is constantly developed, the margin being only slightly angular.

DIMENSIONS. Range of observed specimens: shell length 32 (43) 56 μ, width 27 (42·1) 57 μ, maximum length of spines 2·5 (3·7) 5 μ. Number of specimens measured, 21.

REMARKS. The Cenomanian specimens examined strongly resemble the type material from the Cambridge Greensand and Chalk Marl (Lower Cenomanian) of Cambridgeshire, England. In the lower horizons of the Cenomanian the sulcus, although always present, is not so clearly defined as in higher horizons.

OCCURRENCE. *E. spinosa* is a rare to common species in the lower and middle horizons of the Cenomanian of Fetcham Mill, Compton Bay and Escalles. It is absent from samples FM 690, 670, 650; CB 13, 15, 17, 19, 21; and E 159, 153. It has only beeen observed in one North American sample—sample Sas 1023 (Saskatchewan, Albian).

Cyst-Family **HYSTRICHOSPHAERIDIACEAE** Evit emend. Sarjeant & Downie 1966

Genus ***HYSTRICHOSPHAERIDIUM*** Deflandre emend. Davey & Williams 1966

Hystrichosphaeridium tubiferum (Ehrenberg)

(Pl. 5, figs. 5, 8)

1838 *Xanthidium tubiferum* Ehrenberg : pl. 1, fig. 16.
1966*b* *Hystrichosphaeridium tubiferum* (Ehr.) Davey & Williams : 56, pl. 6, figs. 1, 2; pl. 8, fig. 5; pl. 10, fig. 2; text-fig. 13. (See also for earlier references).

DIMENSIONS. Range of observed specimens: diameter of central body 28 (38·1) 51 μ, maximum length of processes 15 (25·0) 37 μ. Number of specimens measured, 26.

REMARKS. *H. tubiferum* is an infrequent to common species at all horizons throughout the Cenomanian of Fetcham Mill, Compton Bay and Escalles. It is also recorded from the Albian (sample FM 886) and Turonian (sample FM 520) of Fetcham Mill. This species was not recorded in the North American material. Thus the earliest recording of *H. tubiferum* is from the Albian; it ranges throughout the Upper Cretaceous and has been recorded from the Eocene (Ypresian) by Davey & Williams (1966*b*). It is a long-ranging species of little stratigraphic value.

Hystrichosphaeridium deanei Davey & Williams

(Pl. 4, fig. 1)

1966*b* *Hystrichosphaeridium deanei* Davey & Williams : 58, pl. 6, figs. 4, 8.
1967 *Hystrichosphaeridium stellatum* Maier; Clarke & Verdier: 55, pl. 12, figs. 1, 2.

DIMENSIONS. Range of observed specimens: diameter of central body 37 (45·7) 54 μ, maximum length of processes 22 (35·8) 45 μ. Number of specimens measured, 10.

REMARKS. One specimen, occurring in sample E 207 (Escalles), possesses broad processes and appears to occupy a position midway between *H. deanei* and *H. tubiferum*.

OCCURRENCE. *H. deanei* is a rare species confined to the Middle and Upper Cenomanian of Fetcham Mill, Compton Bay and Escalles (Table 25). The samples in which it first occurs are FM 710 (Fetcham Mill), CB 13 (Compton Bay) and E 195 (Escalles). *H. deanei* has also been recorded from the Turonian sample FM 520, from Fetcham Mill. It is absent from the North American material.

Hystrichosphaeridium readei Davey & Williams

1966*b* *Hystrichosphaeridium readei* Davey & Williams : 64, pl. 6, fig. 3 (See also for earlier references).

DIMENSIONS. Range of observed specimens: diameter of central body 31 (42·1) 57 μ, maximum length of processes 23 (29·7) 35 μ. Number of specimens measured, 11.

OCCURRENCE. *H. readei* is very rare in samples FM 810, 790, 770 (Fetcham Mill) and E 207 (Escalles); and it is rare to infrequent in samples FM 690, 670, E 183, 177, 165, 159 and CB 9 (Compton Bay). Two specimens were recorded in the Albian sample (FM 886) from Fetcham Mill. This species was not recorded in the North American samples.

Hystrichosphaeridium radiculatum Davey & Williams

(Pl. 4, fig. 8)

1966*b* *Hystrichosphaeridium radiculatum* Davey & Williams : 65, pl. 7, fig. 9; pl. 9, fig. 6.

DIMENSIONS. Range of observed specimens: diameter of central body 27 (38·8) 43 μ, maximum length of processes 12 (15·9) 20 μ. Number of specimens measured, 11.

OCCURRENCE. *H. radiculatum* is a very rare to infrequent species occurring at a number of horizons throughout the Cenomanian of Fetcham Mill, Compton Bay and Escalles. It has also been recorded in the Albian sample from Fetcham Mill (sample FM 886), but is absent from the North American material.

Hystrichosphaeridium mantelli Davey & Williams

(Pl. 4, fig. 9)

1966*b* *Hystrichosphaeridium mantelli* Davey & Williams : 66, pl. 6, fig. 6.

DIMENSIONS. Range of observed specimens: diameter of central body 32 (38·6) 48 μ, maximum length of processes 12 (21·4) 26 μ. Number of specimens measured, 15.

REMARKS. The reticulate nature of the central body and the fibrous processes differentiate *H. mantelli* from most previously described species. *H. radiculatum* is the most similar but differs from *H. mantelli* by the more branched and deeply furcate processes and the tendency for the fibrils of the processes to continue across the surface of the central body.

OCCURRENCE. *H. mantelli* is a very rare to infrequent species occurring in most samples throughout the Cenomanian of Fetcham Mill, Compton Bay and Escalles. It has also been recorded in the Turonian sample from Fetcham Mill (sample FM 520), but is absent from the North American material.

Hystrichosphaeridium bowerbanki Davey & Williams

(Pl. 5, fig. 9)

1966*b* *Hystrichosphaeridium bowerbanki* Davey & Williams : 69, pl. 8, figs. 1, 4.

DIMENSIONS. Range of observed specimens: diameter of central body 25 (31·9) 40 μ, maximum length of processes 20 (25·5) 28 μ. Number of specimens measured, 10.

REMARKS. *H. bowerbanki* is rare to infrequent in six Middle Cenomanian samples—FM 770, 750, 730 and 690 from Fetcham Mill and CB 9, and 17 from Compton Bay. It has also been recorded from the Albian sample (FM 886) and the Turonian sample (FM 520), both from Fetcham Mill.

Hystrichosphaeridium difficile Manum & Cookson

(Pl. 4, figs. 2, 6, 7)

1964 *Hystrichosphaeridium difficile* Manum & Cookson : 12, pl. 3, figs. 1–3, 7.

DESCRIPTION. The shell is subspherical, sometimes with a small apical prominence; shell wall thick (*c.* 1 μ), smooth to lightly granular. The processes, approximately 30 in number, are complex, usually broadly tubiform or buccinate in shape, of constant length on any specimen but variable in width (3 to 18 μ). Distally the larger processes have a rectangular opening, with a serrate margin which gives rise to four broad spines. Typically there are four bands of thickening extending along the length of the processes and passing onto the shell surface. There, each joins with a similar thickening from a neighbouring process, thus forming a coarse reticulation on the shell surface. The large tubular processes are arranged in a circular manner around the shell, reflecting the precingular, cingular and postcingular series of plates. Fine processes are uncommon and may be sulcal in position. An apical archaeopyle is typically developed and possesses an angular margin marked at intervals with V-shaped notches. Although often remaining attached, isolated operculae have been identified (Pl. 4, figs. 6, 7) and bear four moderate-sized tubular processes.

Dimensions. Range of observed specimens: diameter of central body 49 (64·9) 79 μ, maximum length of processes 18 (24·5) 31 μ. Number of specimens measured, 8.

Remarks. The specimens studied are extremely similar to the type material of Lower Cretaceous age described by Manum & Cookson (1964) from Arctic Canada. The only difference appears to be that in the type material the shell surface has a fine reticulation which is absent from the specimens studied.

Two similar species are *H. costatum* Davey & Williams (1966*b*) from the Oxford Clay of England and *H. readei* Davey & Williams (1966*b*) from the Cenomanian of England. However, both species are considerably smaller than *H. difficile* and possess narrower and less complex processes.

Occurrence. *H. difficile* has only been recorded from the Saskatchewan material. It is infrequent in samples Sas 1084 (Albian) and Sas 890 (Cenomanian), and common in sample Sas 805 (Cenomanian).

Genus ***OLIGOSPHAERIDIUM*** Davey & Williams 1966

Oligosphaeridium complex (White)

(Pl. 5, figs. 6, 7)

1842 *Xanthidium tubiferum complex* White : 39, pl. 4, div. 3, fig. 11.

1966*b* *Oligosphaeridium complex* (White) Davey & Williams : 71, pl. 7, figs. 1, 2; pl. 10, fig. 3; text-fig. 14 (See also for earlier references).

1967 *Hystrichosphaeridium complex* (White) Clarke & Verdier: 53, pl. 11, figs. 10, 11.

Dimensions. Range of observed specimens: diameter of central body 34 (41·1) 55 μ, maximum length of processes 22 (34·6) 43 μ. Number of specimens measured, 12.

Remarks. Davey & Williams described examples of *O. complex* from the Speeton Clay (Barremian), Lower Chalk (Cenomanian) and London Clay (Ypresian), all from England.

Occurrence. *O. complex* is a rare to common species in all samples from Fetcham Mill, Compton Bay and Escalles. It is also present in the Albian sample (FM 886) and the Turonian sample (FM 520) both from Fetcham Mill. This species is present in the Albian and the lowermost Cenomanian sample from Saskatchewan—Sas 1084 1023, 967, and 890—but is absent from the Texas samples.

O. complex thus has a known stratigraphic range from the Neocomian (Gocht 1959; Cookson & Eisenack 1958) to the Eocene, Ypresian (Davey & Williams 1966*b*).

Oligosphaeridium reticulatum Davey & Williams

1966*b* *Oligosphaeridium reticulatum* Davey & Williams : 74, pl. 7, fig. 10.

Dimensions. Range of observed specimens: diameter of central body 29–47 μ, length of processes 14–26 μ. Number of specimens measured, 5.

Occurrence. *O. reticulatum* is an infrequent species occurring in the two lower samples from Fetcham Mill, samples FM 840 and 810.

Oligosphaeridium prolixispinosum Davey & Williams

(Pl. 5, fig. 4)

1966*b* *Oligosphaeridium prolixispinosum* Davey & Williams : 76, pl. 8, figs. 2, 3.

Dimensions. Range of observed specimens: length of central body 33 (39·0) 43 μ, width 20 (28·7) 34 μ, maximum length of processes 18 (25·0) 30 μ. Number of specimens measured, 15.

Occurrence. *O. prolixispinosum* is a rare species confined mainly to the Lower and Middle Cenomanian of Fetcham Mill and Escalles, although it does occur occasionally in the Upper Cenomanian. This species has only been recorded twice in the samples CB 17 and 21 from Compton Bay, both from the Upper Cenomanian. It has not been recorded in the North American material.

Oligosphaeridium anthophorum (Cookson & Eisenack)

(Pl. 5, figs. 1, 2, 3)

1958 *Hystrichosphaeridium anthophorum* Cookson & Eisenack : 43, pl. 11, figs. 12, 13; text-figs. 16–18.
1958 *Hystrichosphaeridium anthophorum* Cookson & Eisenack; Eisenack, 402, pl. 26, figs. 1, 2.
1961 *Hystrichosphaeridium anthophorum* Cookson & Eisenack; Alberti : 34, pl. 9, fig. 16.
1966*b* *Oligosphaeridium anthophorum* (Cookson & Eisenack) Davey & Williams : 77.

Description. The shell is subspherical; shell wall smooth to lightly granular. An apical archaeopyle is typically developed and possesses an angular margin. The processes are hollow, buccinate to infundibular, with the distal flared portion perforate. Distally the margins of the processes are usually entire, but may bear one or two small spines. A complete specimen possesses 18 processes, reflecting a tabulation characteristic of this genus. The processes are all of equal size except for the first postcingular (1‴) and the posterior intercalary (1p) which are often reduced.

Dimensions. Range of observed specimens: diameter of central body 38 (46·3) 57 μ, maximum length of processes 18 (34·1) 43 μ. Number of specimens measured, 8.

Remarks. The presence of complex perforate processes having an entire distal margin differentiate this species from all other similar forms.

Occurrence. *O. anthophorum* has been recorded from the Upper Jurassic—Lower Cretaceous (Aptian–Albian) of Australia (Cookson & Eisenack 1958), from the Aptian of Germany (Eisenack 1958) and from the Upper Barremian—Albian of Germany (Alberti 1961). This species has been recorded from one sample, Sas 1023, from the Albian of Saskatchewan where it is common.

Oligosphaeridium reniforme (Tasch)

(Pl. 6, fig. 1)

1964 *Hystrichosphaeridium reniforme* Tasch : 193, pl. 2, fig. 6.
1966*b* *Oligosphaeridium reniforme* (Tasch) Davey & Williams : 77.

Description. The shell is subspherical to ovoidal, shell wall lightly granular. The processes are hollow, tubiform, widening distally into a broad, flat-topped funnel. The distal margin of the funnel bears a small number of pointed and irregularly shaped spines. Distally the processes sometimes possess large, subcircular perforations. An apical archaeopyle is typically developed.

Dimensions. Range of observed specimens: diameter of central body 31 (42·4) 49 μ, maximum length of processes 20 (24·9) 30 μ. Number of specimens measured, 7.

Remarks. The specimens appear to be very similar to the type material from the Albian of Kansas although Tasch did not describe the presence of distal perforations. *O. reniforme* differs from *O. anthophorum* and *O. perforatum* (Gocht 1959) by the presence of distal spines. It differs from *O. pulcherrimum* Deflandre & Cookson (1955) in that the processes possess only a few spines, are not so complexly perforate and distally are flat-topped.

Occurrence. *O. reniforme* is infrequent in all the Albian–Cenomanian samples from Saskatchewan. It has not been recorded elsewhere.

Genus ***LITOSPHAERIDIUM*** Davey & Williams 1966

Litosphaeridium siphoniphorum (Cookson & Eisenack)

(Pl. 6, figs. 3, 4; Fig. 15)

1958 *Hystrichosphaeridium siphoniphorum* Cookson & Eisenack : 44, pl. 11, figs. 8–10.
1966*b* *Litosphaeridium siphoniphorum* (Cookson & Eisenack) Davey & Williams : 80, pl. 7, figs. 7, 8; text-figs. 16, 17. (See also for earlier references).
1967 *Hystrichosphaeridium siphoniphorum* Cookson & Eisenack; Clarke & Verdier: 55, pl. 11, figs. 1, 2.

Dimensions. Range of observed specimens: diameter of central body 21 (34·0) 47 μ, length of processes 4–25 μ. Number of specimens measured, 160.

Description. A statistical study was made of this species using 20–30 specimens from each of six samples at 40-foot intervals from the Fetcham Mill Borehole. The purpose of this study was to see if the variation in the mean size of *L. siphoniphorum* was directional, and if there was a significant difference in this measurement for

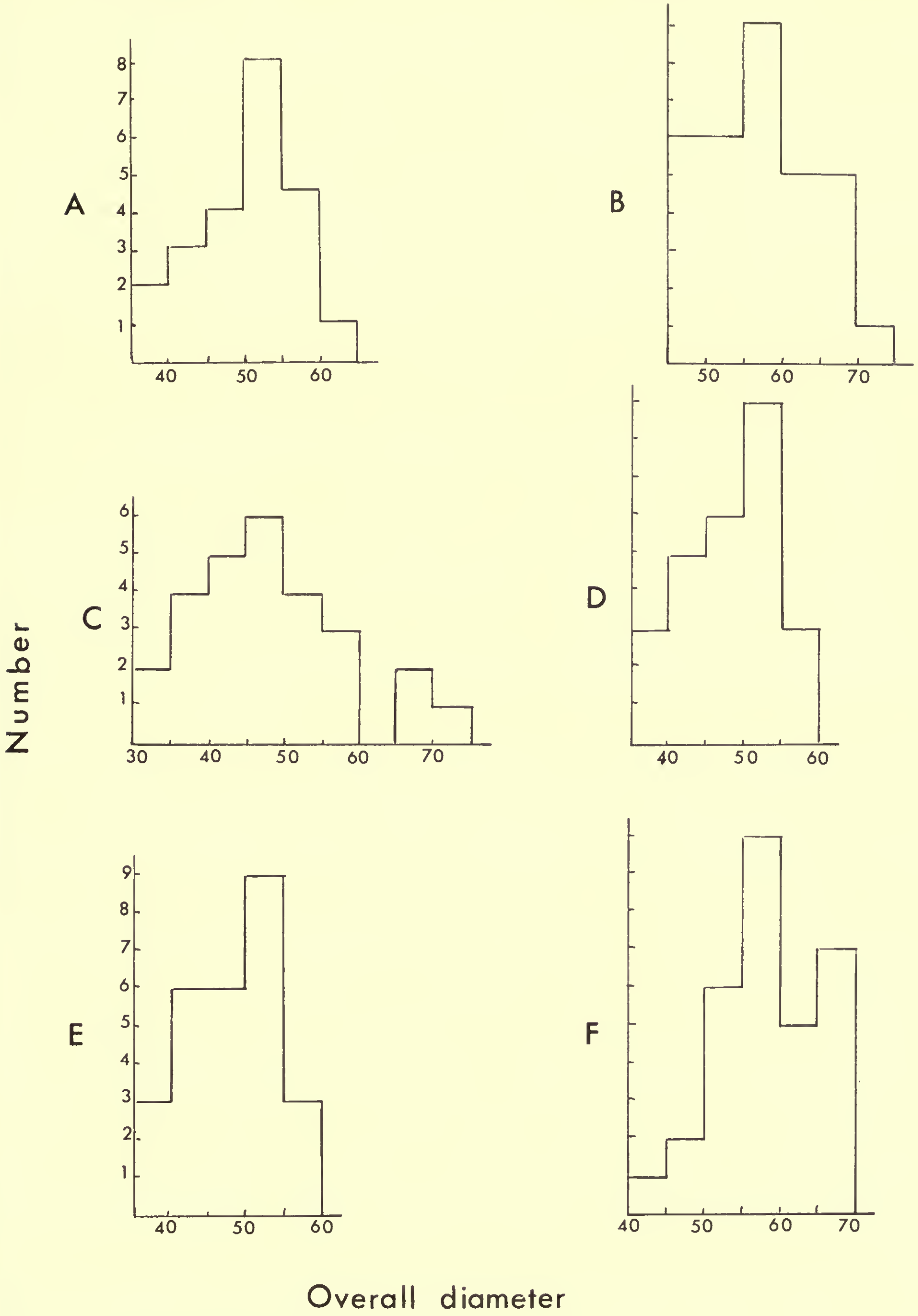

FIG. 15. Overall diameter—frequency histograms of *Litosphaeridium siphoniphorum* (Cookson and Eisenack) at six horizons from Fetcham Mill, Surrey. A. Sample FM 650, B. Sample FM 690, C. Sample FM 730, D. Sample FM 770, E. Sample FM 810, F. Sample FM 840.

successive samples. The measurement taken was the overall diameter. The position of the archaeopyle is always obvious, allowing easy specimen orientation. Thus to make all measurements strictly comparable the overall diameter was always taken in the plane of the archaeopyle.

Histograms (Fig. 15) were drawn for each assemblage. The mean overall diameter for each assemblage varied for each horizon but, unfortunately, the variation was not directional and, therefore, was of little stratigraphic value. The Student's t-test was performed on successive pairs of assemblages to see whether or not they were significantly different (Table A). A probability of 0·05 or less was taken as being significant.

TABLE A

FM 650 FM 690	$(\bar{x} = 50\cdot 0\,\mu)$ $(\bar{x} = 56\cdot 6\,\mu)$	$t = 3\cdot 08$	(significant difference)
FM 690 FM 730	$(\bar{x} = 56\cdot 6\,\mu)$ $(\bar{x} = 48\cdot 3\,\mu)$	$t = 3\cdot 16$	(significant difference)
FM 730 FM 770	$(\bar{x} = 48\cdot 3\,\mu)$ $(\bar{x} = 48\cdot 1\,\mu)$	$t = 0\cdot 084$	(no significant difference)
FM 770 FM 810	$(\bar{x} = 48\cdot 1\,\mu)$ $(\bar{x} = 48\cdot 1\,\mu)$	$t = 0$	(no significant difference)
FM 810 FM 840	$(\bar{x} = 48\cdot 1\,\mu)$ $(\bar{x} = 58\cdot 0\,\mu)$	$t = 5\cdot 4$	(significant difference)

The results show that there is a significant difference at the 5% level between some of the assemblages with respect to this character. However, all the specimens measured were apparently morphologically identical and differ only in size. Specimens from one sample vary considerably in size but were probably formed by one species of motile dinoflagellate. Thus the size of *L. siphoniphorum* appears to be quite variable and should, at the moment, not be used as a diagnostic feature for the subdivision of this species. The reason for the means in successive samples to be significantly different is probably because of palaeoecological changes in the environment.

REMARKS. All the specimens of *L. siphoniphorum* examined agree fairly closely with the type material from Australia. The Surrey specimens appear to be smaller, but the range of the Australian forms was not given so no true size comparison can be made.

OCCURRENCE. *L. siphoniphorum* is rare to common at all horizons throughout the Cenomanian of Fetcham Mill, Compton Bay and Escalles. It is present in the Albian sample FM 866, but absent from the Turonian sample, FM 520. It is rare to infrequent in the lower four samples from Saskatchewan—samples Sas 1084, 1023, 967 and 890. This species is also present in the Upper Woodbine Formation of Texas. Thus *L. siphoniphorum* has a wide geographical distribution and a fairly restricted range. It has been recorded from the Albian of Australia, Rumania, Canada and Britain and from the Cenomanian of Australia, Canada and Britain.

Genus ***POLYSPHAERIDIUM*** Davey & Williams 1966

Polysphaeridium pumilum Davey & Williams

?1955 *Hystrichosphaeridium recurvatum* White; Deflandre & Cookson : 269, pl. 1, fig. 12.
1966*b* *Polysphaeridium pumilum* Davey & Williams : 93, pl. 7, figs. 3, 4.

DIMENSIONS. Range of observed specimens: overall diameter 30–40 μ, diameter of central body 17–25 μ, length of processes 7–10 μ, width of processes 1–1·5 μ, number of processes 38–44. Number of specimens measured, 3.

OCCURRENCE. Only three specimens of *P. pumilum* have been observed, one from sample FM 750 and two from sample FM 770.

Polysphaeridium laminaspinosum Davey & Williams

(Pl. 4, figs. 10, 11)

1966*b* *Polysphaeridium laminaspinosum* Davey & Williams : 94, pl. 8, fig. 8.

DIMENSIONS. Range of observed specimens: diameter of central body 20 (26·8) 29 μ, maximum length of processes 9 (13·7) 17 μ. Number of specimens measured, 8.

OCCURRENCE. *P. laminaspinosum* is rare to very rare, occurring spasmodically throughout the Cenomanian of Fetcham Mill, Compton Bay and Escalles. It has not been recorded elsewhere.

Genus ***TANYOSPHAERIDIUM*** Davey & Williams 1966

Tanyosphaeridium variecalamum Davey & Williams

(Pl. 6, figs. 2, 5)

1966*b* *Tanyosphaeridium variecalamum* Davey & Williams : 98, pl. 6, fig. 7; text-fig. 20.

DIMENSIONS. Range of observed specimens: length of central body 27 (32·3) 43 μ, width 14 (20·1) 24 μ, maximum length of processes 11 (15·0) 24 μ. Number of specimens measured, 14.

OCCURRENCE. *T. variecalamum* is a rare to infrequent species at most horizons throughout the Cenomanian of Fetcham Mill, Compton Bay and Escalles. It is also present in the Albian sample, FM 886, and the Turonian sample, FM 520, both from Fetcham Mill. One specimen was located in the Saskatchewan material, from the Albian sample Sas 1084.

Genus ***CALLAIOSPHAERIDIUM*** Davey & Williams 1966

REMARKS. *Hexasphaera* Clarke & Verdier (1967; 42) is a junior synonym of *Callaiosphaeridium*.

Callaiosphaeridium asymmetricum (Deflandre & Courteville)

(Pl. 6, fig. 6)

1939 *Hystrichosphaeridium asymmetricum* Deflandre & Courteville : 100, pl. 4, figs. 1, 2.

1966*b* *Callaiosphaeridium asymmetricum* (Deflandre & Courteville) Davey & Williams : 104, pl. 8, figs. 9, 10; pl. 9, fig. 2.

1967 *Hexasphaera asymmetrica* (Deflandre & Courtville) Clarke & Verdier: 43, pl. 7, figs. 1–3 text-fig. 17.

DIMENSIONS. Range of observed specimens: diameter of central body 37 (45·8) 58 μ, maximum length of cingular processes 10 (25·0) 32 μ. Number of specimens measured, 6.

REMARKS. The author disagrees with the description of Clarke & Verdier (1967) in that the archaeopyle is epitractal, not apical, and that the antapical plate is five-sided, not six-sided, bearing a process at each corner. The position of the three sutural crests separating the large plates has, however, been verified.

OCCURRENCE. *C. asymmetricum* is rare to infrequent at most horizons throughout the Cenomanian of Fetcham Mill, Compton Bay and Escalles. It has been recorded in the Albian sample FM 886 and the Turonian sample FM 520, both from Fetcham Mill, but is absent from the North American material.

Genus ***CLEISTOSPHAERIDIUM*** Davey, Downie, Sarjeant & Williams 1966

Cleistosphaeridium heteracanthum (Deflandre & Cookson)

(Pl. 7, fig. 8)

1955 *Hystrichosphaeridium heteracanthum* Deflandre & Cookson : 276, pl. 2, figs. 5, 6; text-figs. 40, 41.

1966 *Cleistosphaeridium heteracanthum* (Deflandre & Cookson) Davey, Downie, Sarjeant & Williams : 168, pl. 2, figs. 6, 7 (See also for earlier references).

DIMENSIONS. Range of observed specimens: shell diameter 42 (53·2) 63 μ, maximum length of processes 9 (13·8) 17 μ. Number of specimens measured, 9.

OCCURRENCE. *C. heteracanthum* is a rare species restricted to the Upper Cenomanian—samples FM 690, 670 and 650 from Fetcham Mill, samples CB 19 and 21 from Compton Bay and sample E 153 from Escalles. It was not recorded from North America.

Cleistosphaeridium multifurcatum (Deflandre)

(Pl. 8, figs. 7, 10)

1937 *Hystrichosphaeridium multifurcatum* Deflandre : 76, pl. 16, figs. 1–3.

1939 *Hystrichosphaeridium multifurcatum* Deflandre; Deflandre & Courteville : 102, pl. 3, fig. 2.

1952 *Hystrichosphaeridium multifurcatum* Deflandre; W. Wetzel : 400, text-fig. 16.

1955 *Hystrichosphaeridium multifurcatum* Deflandre; Valensi : 588, pl. 1, fig. 21; pl. 5, fig. 5.

1960 *Baltisphaeridium multifurcatum* (Deflandre) Klement : 59.

1963 *Hystrichosphaeridium multifurcatum* Deflandre; Górka : 66, pl. 9, figs. 4–6; text-fig. 8, fig. 1.
1966 *Cleistosphaeridium multifurcatum* (Deflandre) Davey, Downie, Sarjeant & Williams: 170.

DIMENSIONS. Range of observed specimens: diameter of central body 39 (55·0) 68 μ, maximum length of processes 8 (11·2) 13 μ. Number of specimens measured, 8.

OCCURRENCE. *C. multifurcatum* is rare at most horizons in the Cenomanian of Fetcham Mill, Compton Bay and Escalles. In a few Upper Cenomanian samples (FM 690, 670 and 650; CB 19, 21 and E 153) it is completely absent. In these samples it seems to be replaced by *C. heteracanthum*. *C. multifurcatum* was not observed in the North American samples.

Cleistosphaeridium armatum (Deflandre) comb. nov.

(Pl. 8, figs. 1, 2, 12)

1937 *Hystrichosphaeridium armatum* Deflandre : 76, pl. 16, figs. 6, 7.
1947 *Hystrichosphaeridium armatum* Deflandre; Deflandre: fig. 1, No. 10.
1952*a* *Hystrichosphaeridium armatum* Deflandre; Deflandre: fig. 14.
1963 *Baltisphaeridium armatum* (Deflandre) Downie & Sarjeant : 91.
1967 *Baltisphaeridium armatum* (Deflandre) Clark & Verdier: 71, pl. 13, fig. 3.

EMENDED DIAGNOSIS. Shell subspherical; shell wall of moderate thickness, densely granular. Processes numerous, fairly broad, rigid, tapering gradually distally. Proximally processes possess longitudinal basal striations; distally simple or giving rise to variable number of small spines. Apical archaeopyle occasionally developed.

HOLOTYPE. Slide AJ. 54, Laboratoire de Micropaléontologie, École Practique des Hautes Études, Paris. (Figured by Deflandre 1937, pl. 16, fig. 6). Upper Cretaceous flint from the Paris Basin.

DIMENSIONS. Holotype: shell length 20 μ, width 18–20 μ, length of processes 10–15 μ. Range of Cenomanian specimens: diameter of central body 19 (30·8) 42 μ, maximum length of processes 5 (9·6) 16 μ. Number of specimens measured, 33.

DESCRIPTION. The granules are elongate (*c.* 0·1–0·5 μ in height) so giving the shell surface the appearance of possessing a matting of short hairs. This ornamentation, commented on by Deflandre in the original description of this species, was verified by the present author when examining the type material in Paris.

The processes are all of a similar length on any one specimen and may vary in width from 1 to 3 μ. They are hollow, always closed distally terminating either simply (the extremity may be recurved) or more commonly the distal one quarter of the processes bear a small number of stiff spines (pl. 8, fig. 2). The opening, when observable, possesses an angular margin characteristic of an apical archaeopyle.

REMARKS. The specimens studied strongly resemble *C. armatum* as described by Deflandre from Upper Cretaceous flints, one of which was of Cenomanian age. The appearance of the shell surface and form of the processes make this an easily recognizable species.

OCCURRENCE. *C. armatum* is common at all horizons throughout the Cenomanian of Fetcham Mill, Compton Bay and Escalles. It is also present in the Upper Woodbine and Lower Eagle Ford formations of Texas, but has not been observed in the Saskatchewan samples.

Cleistosphaeridium polypes (Cookson & Eisenack) comb. nov.

(Pl. 6, figs. 7, 8)

1962*b* *Hystrichosphaeridium recurvatum* subsp. *polypes* Cookson & Eisenack : 491, pl. 4, figs. 11–13.

Description. The shell is spherical to subspherical and bears numerous slender processes. The shell wall is thin and may be smooth or slightly granular. The processes are narrow, usually less than 1 μ in width for most of their length, broadening slightly proximally. They are closed distally and terminate in a number of short, fine spines. The latter are not so numerous in the English and French specimens as in those from Australia and North America where the distal spines are numerous. A fairly large archaeopyle, probably apical, with an angular margin is often present.

Dimensions. Range of observed specimens: shell diameter 31 (38·4) 47 μ, maximum length of processes 9 (13·4) 18 μ. Number of specimens measured, 20.

Remarks. *C. polypes* was originally described by Cookson & Eisenack from the Aptian–Cenomanian of Australia and was considered to be a subspecies of *Hystrichosphaeridium recurvatum* (White). The resemblance between the two forms is very slight and they are not considered to be closely related. *C. polypes* is placed in this genus because of the presence of numerous closed processes and the probable apical location of the archaeopyle.

Occurrence. *C. polypes* is a very rare species restricted to the Middle and Upper Cenomanian of Fetcham Mill (samples FM 750, 730), Compton Bay (samples CB 9, 17, 21) and Escalles (samples E 189, 177, 165). It is common in the Upper Woodbine formation of Texas, and is present in one sample from Saskatchewan (sample Sas 835).

Cleistosphaeridium polypes var. ***clavulum*** nov.

(Pl. 6, figs. 9, 10)

1964 *Hystrichosphaeridium recurvatum* subsp. *polypes* Cookson & Eisenack; Cookson & Hughes : 47, pl. 9, fig. 14.

Derivation of name. Latin, *clavulus*, small nail—with reference to the pin-like shape of the processes.

Diagnosis. A variety of *C. polypes* possessing fine, capitate processes. Processes terminating with fine spines are extremely rare.

Type. G.S.M. slide PF 3995(1). Lower Chalk, H.M. Geological Survey Borehole, Fetcham Mill, Surrey at 840 feet depth. Upper Cretaceous (Cenomanian).

Dimensions. Type: diameter of central body 29 by 32 μ, length of processes 12–13 μ. Range: diameter of central body 29 (31·5) 39 μ, maximum length of processes 13 (14·7) 15 μ. Numbers of specimens measured, 10.

REMARKS. *C. polypes* var. *clavulum* differs from *C. polypes* in that the processes are capitate, the terminal bulge being flattened and resembling the head of a pin. Two specimens have been observed each possessing one process of the type characteristic of *C. polypes* thus indicating a relationship between the two forms. *C. polypes* probably evolved from this variety, spiny processes replacing the capitate ones.

OCCURRENCE. This variety has only been recorded from the lowermost Cenomanian samples at Fetcham Mill (sample FM 840) and Compton Bay (sample CB 1). It was previously recorded by Cookson & Hughes (1964) from the Upper Albian—basal Cenomanian of England and so appears to be of stratigraphic importance in England for indicating the base of this stage. It does not occur in the lowermost sample from Escalles.

Cleistosphaeridium huguonioti (Valensi) comb. nov.

(Pl. 7, fig. 10)

1955 *Hystrichosphaeridium huguonioti* Valensi : 38, fig. 2a.
1960*a* *Hystrichosphaeridium ancoriferum* Cookson & Eisenack : 8, pl. 2, fig. 11.
1963 *Hystrichosphaeridium ancoriferum* Cookson & Eisenack; Balteş : 586, pl. 6, fig. 13.
1964 *Hystrichosphaeridium ancoriferum* Cookson & Eisenack; Cookson & Hughes : 47, pl. 9, fig. 7.
1964 *Chlamydophorella nyei* Cookson & Eisenack; Cookson & Hughes : 54, pl. 6, fig. 12.
1966 *Cleistosphaeridium ancoriferum* (Cookson & Eisenack) Davey, Downie, Sarjeant & Williams: 167, pl. 9, fig. 1.
1967 *Hystrichosphaeridium huguonioti* Valensi; Clarke & Verdier: 54, pl. 11, fig. 4, 5.

DESCRIPTION. The shell is subspherical; the shell wall is smooth and gives rise to numerous bifurcating processes which are not aligned to any noticeable extent. Most of the specimens possess an apical archaeopyle, the shape of which is usually difficult to determine because of distortion. However, detached apical regions are common and are 6-sided. The processes are hollow, the central cavity often being constricted to some extent along its length, and closed distally and proximally. The sides of the processes are practically parallel, diverging slightly proximally before joining the shell. Distally they give rise to two slightly recurved spines. Cookson & Eisenack comment on the " transparent tips " of the processes. The extremities of the processes are in fact closed by a thin, transparent membrane. The processes may be isolate or a few may be linked together distally by their spines. The shell wall rarely forms a small rounded apical bulge.

DIMENSIONS. Range of observed specimens: diameter of central body 20 (31·8) 45 μ, length of processes up to 8 μ. Number of specimens measured, 30.

REMARKS. Cookson & Hughes (1964) described *C. huguonioti* and *Chlamydophorella nyei* from the Upper Albian and Lower Cenomanian of England, distinguishing the latter, with difficulty, by the presence of an outer membrane and an apical bulge. After a detailed examination of numerous Cenomanian specimens it was concluded that *Chlamydophorella nyei* s.s., as described from Australia, does not occur in the English and French Cenomanian and that *C. nyei* as described by Cookson &

Hughes belongs in *Cleistosphaeridium huguonioti*. *C. huguonioti* does occasionally appear to possess a membrane linking some of the processes when their spines are joined distally, and an apical prominence may also rarely be present. Some specimens possess joined processes but apparently no apical prominence, whereas others possess an apical prominence but no joined processes. The presence of distinctive bifurcate processes and an apical prominence indicates that *C. huguonioti* is related to *Chlamydophorella*, the outer membrane of the latter being reduced to a small, transparent membrane at the distal end of each process.

OCCURRENCE. *C. huguonioti* is common throughout the Cenomanian of Fetcham Mill, Compton Bay and Escalles (Fig. 22). It is absent from the uppermost sample from Escalles (sample E 153) and from the Turonian sample FM 520. In the Upper Cenomanian at these localities *C. huguonioti* tends to be replaced by its variety, *C. huguonioti* var. *pertusum* nov., which appears to become more abundant as *C. huguonioti* declines. It is present in the Albian sample FM 886 and is common in the Upper Woodbine and Lower Eagle Ford formations of Texas, but was not observed in the Saskatchewan material. This species was first recorded from the Albian–Cenomanian of Australia and is also present in the Albian–Cenomanian of Rumania (Balteş, 1963). Thus *C. huguonioti* appears to be wide-spread geographically and restricted to the Albian and Cenomanian.

Cleistosphaeridium huguonioti var. ***pertusum*** nov.

(Pl. 7, figs. 6, 7, 9)

DERIVATION OF NAME. Latin, *pertusum*, perforated—with reference to the perforate appearance of the processes.

DIAGNOSIS. A variety of *C. huguonioti* possessing spherical to subspherical, smooth walled shell bearing numerous processes. Processes broad-based, tapering distally and terminating with two small recurved spines. Lumen of processes restricted by transverse septa.

HOLOTYPE. G.S.M. slide PF 3040(2). Lower Chalk, H.M. Geological Survey Borehole, Fetcham Mill, Surrey at 670 feet depth. Upper Cretaceous (Cenomanian).

DIMENSIONS. Holotype: diameter of central body 36 by 36 μ, length of processes 7–9 μ, maximum width of processes distally 2 μ. Range: diameter of central body 24 (34·1) 46 μ, length of processes 6 (8·7) 11 μ, maximum width of processes distally 1 (2·7) 4·5 μ. Number of specimens measured, 24.

DESCRIPTION. The processes taper distally from a fairly broad base (2·5–4 μ in width) to a narrow neck (*c.* 0·5 μ in width) before bifurcating to give two short, recurved spines. The processes are hollow but the lumen is traversed by a number of small septa which thus subdivide it, giving the processes a " holey " or vacuolated appearance. An archaeopyle is only rarely observable.

REMARKS. This variety differs from *C. huguonioti* in the form of its processes which are vacuolated, tend to be longer and bear relatively small distal spines. *C. huguonioti* found in the same samples possesses processes which are considerably wider distally (5·5–7·5 μ). *C. huguonioti* var. *pertusum* appears to have evolved from *C. huguonioti* in the Middle to Upper Cenomanian.

OCCURRENCE. *C. huguonioti* var. *pertusum* occurs only in the Upper Cenomanian, where it is common at all horizons. It first occurs in samples FM 710 (Fetcham Mill), CB 15 (Compton Bay) and E 171 (Escalles). At these horizons it is occasionally difficult to distinguish from *C. huguonioti*. Like *C. huguonioti*, this variety is absent from sample E 153 (Escalles) and FM 520 (Fetcham Mill, Turonian). It has not been observed in the samples from North America.

?*Cleistosphaeridium flexuosum* Davey, Downie, Sarjeant & Williams

(Pl. 7, figs. 4)

1966 ? *Cleistosphaeridium flexuosum* Davey, Downie, Sarjeant & Williams: 169, pl. 2, fig. 5.

OCCURRENCE. This is a very rare species occurring at most horizons throughout the Cenomanian of Fetcham Mill. It has not been recorded elsewhere.

?*Cleistosphaeridium parvum* sp. nov.

(Pl. 7, figs. 11, 12)

DERIVATION OF NAME. Latin, *parvus*, little—with reference to the small size of this cyst.

DIAGNOSIS. Shell ovoidal, small; shell wall smooth, bearing numerous long, fine spines. Spines may be aligned along upper and lower boundaries of cingulum. Cingulum strongly laevo-rotatory. Apical archaeopyle typically developed.

HOLOTYPE. B.M. (N.H.) V.51981 (3). Lower Chalk, Bureau de Recherches Géologique et Minières Borehole, Escalles, Pas de Calais at 165 metres depth. Upper Cretaceous (Cenomanian).

DIMENSIONS. Holotype: length of central body 12 μ, width 11 μ, length of processes 6–11 μ. Range: length of central body 11–14 μ, width 10–13 μ, length of processes 6–12 μ. Number of specimens measured, 5.

DESCRIPTION. The spines are long, very fine, terminate distally in a point and widen only slightly when joining the shell. The cingulum is not always observable but some alignment of the spines parallel to the archaeopyle margin is usually present.

REMARKS. ?*C. parvum* resembles only one previously described species, that is *Palaeostomocystis echinulata* Deflandre (1937) from the Upper Cretaceous of France. This species differs in that there are fewer spines (*c.* 12), but is similar in its ovoidal shape, apical archaeopyle, cingulum and small size (6–7 μ long).

The presence of a cingulum has not previously been observed in members of *Cleistosphaeridium* and might later be used as a character in generic subdivision. However, difficulty of observation makes it of dubious value.

OCCURRENCE. ?*C. parvum* is fairly common in three Upper Cenomanian samples from Escalles—E 171, 165 and 159. It has also been observed in a single Lower Cenomanian sample from Compton Bay (CB 5). In all other samples it appears to be absent.

?*Cleistosphaeridium aciculare* sp. nov.

(Pl. 6, figs. 11, 12)

DERIVATION OF NAME. Latin, *acicularis*, like a needle—with reference to the acuminate shape of the processes.

DIAGNOSIS. Shell spherical to subspherical; shell wall of moderate thickness, densely granular. Processes numerous, finely to broadly acuminate, slightly flexuous, less than one-third of shell diameter in length.

HOLOTYPE. B.M. (N.H.) slide V. 51979 (3). Second White Speckled Shale, International Yarbo Borehole No. 17, Saskatchewan at 835 feet depth. Upper Cretaceous (Cenomanian).

DIMENSIONS. Holotype: diameter of central body 43 by 50 μ, length of processes 12–14 μ. Range: diameter of central body 32 (43·0) 54 μ, maximum length of processes 8 (13·9) 21 μ. Number of specimens measured, 11.

DESCRIPTION. The processes may be finely or broadly acuminate but on each individual their width is constant. On individuals bearing fine processes these are more densely packed than in individuals with broad processes. All intergradations exist between the fine and the broad processed forms. The processes are always pointed distally and occasionally bear small subsidiary spines near their extremities. An archaeopyle has never been observed.

REMARKS. ?*C. aciculare* is only tentatively placed in this genus, for although it resembles other members in overall appearance, an apical archaeopyle has not been observed. The numerous acuminate processes and the densely granular shell surface differentiate ?*C. aciculare* from most previously described forms. Most similar seems to be *Exochosphaeridium* (*Hystrichosphaeridium*) cf. *striolatum* (Deflandre) as illustrated by Górka (1963, pl. 10, fig. 6) from the Cenomanian of Poland.

OCCURRENCE. ?*C. aciculare* is common in the following samples from Saskatchewan—Sas 1084, 1023 and 967 (all Albian) and Sas 835 (Cenomanian). It has not been recorded elsewhere.

Genus ***SURCULOSPHAERIDIUM*** Davey, Downie, Sarjeant & Williams 1966

Surculosphaeridium longifurcatum (Firtion)

(Pl. 8, fig. 9)

1952 *Hystrichosphaeridium longifurcatum* Firtion : 157, pl. 9, fig. 1 ; text-fig. 1, H, K, L and M

1963 *Baltisphaeridium longifurcatum* (Firtion) Downie & Sarjeant: 91.

1966 *Surculosphaeridium longifurcatum* (Firtion) Davey, Downie, Sarjeant & Williams : 163, pl. 8, figs. 7, 11; text-figs. 43, 44.

DIMENSIONS. Range of observed forms: lateral view—diameter of central body 30 (38·3) 47 μ; apical view—diameter of central body 36 (42·2) 50 μ, maximum length of processes 14 (22·2) 29 μ. Mean diameter of archaeopyle, 20 μ. Number of specimens measured, 24.

OCCURRENCE. This is a rare species at all horizons throughout the Cenomanian of Fetcham Mill, Compton Bay and Escalles. The only exception is sample FM 730 from Fetcham Mill, where this species is very common, composing 22·5 % of the total microplankton present. The reason for this unusual abundance is unknown. *S. longifurcatum* is also present in the Lower Eagle Ford formation of Texas, but was not observed in the Saskatchewan samples. It has not been observed in the Albian sample (FM 886) or the Turonian sample (FM 520) from Fetcham Mill, and thus appears to be characteristically, Cenomanian.

Genus ***HYSTRICHOKOLPOMA*** Klumpp emend. Williams & Downie 1966

Hystrichokolpoma ferox (Deflandre)

(Pl. 9, figs. 5–7)

1937 *Hystrichosphaeridium ferox* Deflandre : 72, pl. 14, figs. 3, 4.
1966*a* *Hystrichokolpoma ferox* (Deflandre) Williams & Downie : 181.
1967 *Baltisphaeridium ferox* (Deflandre) Clarke & Verdier: 73, pl. 15, fig. 4 (see also for earlier references).

EMENDED DIAGNOSIS. Shell subspherical, densely granular or reticulate. Processes thin walled, granular, often striated, of three kinds: (i) 6 large precingular and 4 large postcingular, possessing wide bases and tapering distally giving rise to 2 or more tubules, typically open; (ii) a single long tubular antapical process and (iii) cingular and sulcal processes, of moderate length, slender and tubular, only joining proximally if at all. Archaeopyle apical.

HOLOTYPE. Slide AH 72, Laboratoire de Micropaléontologie, Ecole Practique des Hautes Etudes, Paris. (Figured by Deflandre 1937*a*, pl. 14, fig. 3). Senonian flint from the Paris Basin.

DIMENSIONS. Holotype: length of shell 46 μ, width 36 μ, overall length 78 μ, length of processes 15–17 μ. Range of Cenomanian specimens: diameter of central body 39 (46·1) 56 μ, maximum length of processes 27 (30·2) 36 μ. Number of specimens measured, 13.

DESCRIPTION. *H. ferox* appears to be a fairly variable species. In some specimens the tabulation is not clearly indicated by the processes which tend to be smaller and may even be closed distally. However, the processes usually are well developed, their bases covering an area of the shell surface which is often slightly raised and of the same shape as a thecal plate. The precingular and postcingular processes are largest and give rise distally to as many as 10 tubules. Each cingular process divides proximally into 2 or 3 long slender tubules aligned along the cingulum. The sulcal processes may proximally divide into two tubules or may consist of a single tubule which is sometimes reduced and closed distally. The antapical process is long, tubular, open distally, and terminates with a smooth or serrate margin.

REMARKS. The Cenomanian specimens closely resemble the holotype of *H. ferox*, which was examined in Paris by the author, by kind permission of Professor Deflandre. The processes of the holotype are of the same form as, and similarly positioned to, those of the Cenomanian forms. The antapical process of the holotype, not shown in Deflandre's illustration (1937, pl. 14, fig. 3), is long and tubular.

OCCURRENCE. *H. ferox* is rare to very rare at most horizons throughout the Cenomanian of Fetcham Mill and Escalles, but has not been observed at Compton Bay or in the North American samples. It is also present in the Turonian sample (sample FM 520) from Fetcham Mill. Hence the stratigraphic range is from Aptian (Eisenack 1958) to Upper Cretaceous, probably Senonian (Deflandre 1937).

Genus ***PROLIXOSPHAERIDIUM*** Davey, Downie, Sarjeant & Williams 1966

DIAGNOSIS. Shell elongate ovoidal to ellipsoidal, one pole (apical) typically lost in archaeopyle formation. Opposite pole occupied by one or two antapical processes. Remaining processes arranged in distinct rows, encircling shell and slightly offset at a position corresponding to sulcus. Number of processes exceeds 30. Processes closed proximally, typically but not constantly closed distally; their distal terminations simple, faring in varied fashion, or briefly furcate. Shell surface sometimes bears cover of coarse granules or very short, simple spinelets.

REMARKS. The diagnosis has been changed slightly: ' typically but not constantly closed distally ' being inserted in place of ' closed or open distally ', with respect to the processes. The processes of *Prolixosphaeridium* usually taper distally and are closed. Specimens with open tubular processes belong to *Tanyosphaeridium* Davey & Williams (1966*b*).

Prolixosphaeridium conulum sp. nov.

(Pl. 8, figs. 5, 6)

DERIVATION OF NAME. Latin, *conulus*, cone—with reference to the rather conical shape of the processes.

DIAGNOSIS. Shell elongate ovoidal; shell wall densely granular and bearing moderate number of processes. Processes acuminate to subconical, smooth walled, typically rigid, pointed distally. Processes tend to be aligned in circular manner around shell. Archaeopyle apical.

HOLOTYPE. B.M. (N.H.) V.51981 (5). Lower Chalk, Bureau de Recherches Géologiques et Minières Borehole, Escalles, Pas de Calais, at 165 metres depth. Upper Cretaceous (Cenomanian).

DIMENSIONS. Holotype: shell length 47 μ, width 27 μ, length of processes 11–16 μ. Range: shell length 38 (43·8) 50 μ, width 20 (25·9) 29 μ, maximum length of processes 11 (15·1) 18 μ. Number of specimens measured, 8.

DESCRIPTION. The length of the shell is slightly less than twice the width. The surface granules are relatively large (*c.* 0·2–0·4 μ in width and height); they are equidistant from one another. The processes (45–60 in number) have broad bases (up to 6 μ) and taper distally to terminate in a point. They are approximately half the shell width in length, hollow and typically rigid, only occasionally being bent near the distal end. In the central region of the shell the processes are aligned, the rows encircling the shell. However, in one longitudinal portion in this region the processes are generally smaller and haphazard in arrangement. This region probably corresponds to the sulcus.

REMARKS. The distinctive shape, number and size of the processes distinguish P. *conulum.* A rather similar but longer form was illustrated by Cookson & Eisenack (1958, pl. 8, fig. 11) as *Hystrichosphaeridium parvispinum* Deflandre. This specimen comes from the Aptian of Australia and is said to grade into forms possessing more numerous processes similar to *P. conulum.* Deflandre's species was placed in *Prolixosphaeridium* by Davey, Downie, Sarjeant & Williams (1966).

Two other species are rather similar. The holotype of *P. granulosum* (Deflandre) measures 18 by 33 μ and possesses 20–30 long processes, the latter being approximately equal to the shell width. The number of processes and the relative lengths of the processes, therefore, differentiate this species from *P. conulum. P. granulosum* as described by Valensi (1955) from the Upper Cretaceous, and Sarjeant (1962) from the Upper Jurassic, are more similar to *P. conulum* but do not possess conical processes.

P. mixtispinosum (Klement) differs from *P. conulum* by possessing two kinds of processes—(i) approximately 50 processes of moderate length and (ii) numerous fine hairs covering the shell surface.

OCCURRENCE. *P. conulum* has only been observed at certain horizons in the Upper Cenomanian of Fetcham Mill, Compton Bay and Escalles—in samples FM 690, CB 19, E 165, E 159 and E 153.

Genus ***CORONIFERA*** Cookson & Eisenack emend.

EMENDED DIAGNOSIS. Shell subspherical to ovoidal, bearing numerous simple or bifurcating processes. Processes solid or hollow, closed distally, and joined proximally by low crests or membranes. Apical process distinctive, simple or branched. Antapical process large, tubular, often terminating with denticulate margin. Archaeopyle apical.

TYPE SPECIES. *Coronifera oceanica* Cookson & Eisenack 1958. Lower Cretaceous (Albian); Australia.

REMARKS. The diagnosis has been emended to include the presence of an apical archaeopyle and low crests joining the processes, and the positions of the two distinctive processes.

Coronifera differs from *Diphyes* Cookson (1965) in that the processes are never tubular and open distally, and by the presence of a reticulum joining the basal portion of the processes. However, both genera possess a large tubular antapical process and an apical archaeopyle, and are probably closely related.

Coronifera oceanica Cookson & Eisenack

(Pl. 8, figs. 8, 11)

1958 *Coronifera oceanica* Cookson & Eisenack : 45, pl. 12, figs. 5, 6.
1958 *Coronifera oceanica* Cookson & Eisenack; Eisenack : 407, pl. 25, fig. 1.
1964 *Coronifera oceanica* Cookson & Eisenack; Cookson & Hughes : 56, pl. 9, figs. 8, 9.
1967 *Coronifera oceanica* Cookson & Eisenack; Clarke & Verdier: 77, pl. 17, fig. 7.

DESCRIPTION. The shell is subspherical to ovoidal, thin-walled, and bears numerous processes of length between one-quarter and one-third of the shell diameter. There is, occasionally, a slight apical prominence beneath the apical process. Fine fibres radiate from the bases of the processes over the shell surface reminiscent of those on the shell surface of *Exochosphaeridium striolatum* (Deflandre). The processes are weak, fairly flexuous and commonly joined to each other by a network of low crests or fine membranes. The latter may be proximal or may extend along the entire length of the processes. Distally the processes are closed and may be simple, bifurcate or trifurcate. A large tubular process is present at the antapex; it is open distally and terminates with a denticulate margin. At the apex, when attached, there is a process which is only slightly larger than the typical processes but is usually branched and, therefore, distinctive. The large archaeoplye, developed in the majority of specimens, has an angular margin and forms opposite the antapical process.

A number of specimens of *C. oceanica* were observed in the Albian sample from Fetcham Mill (FM 886). They resemble the specimens of Eisenack (1958) from the Aptian of Germany in that the processes are fewer, more solid and are usually simple.

DIMENSIONS. Range of observed specimens: diameter of central body 31 (40) 54 μ, maximum length of processes 11 (15·3) 22 μ. Number of specimens measured, 15.

REMARKS. *C. oceanica* has previously been recorded from the Upper Aptian of Germany (Eisenack, 1958), Albian of Australia (Cookson & Eisenack, 1958) and basal Cenomanian of England (Cookson & Hughes, 1964). The surface reticulation was not described in the Australian type material but appears to be present on the photographed specimens. It was first commented on by Cookson & Hughes.

OCCURRENCE. In addition to the German and Australian records, *C. oceanica* is infrequent to common at all horizons throughout the Cenomanian of Fetcham Mill, Compton Bay and Escalles, and is also common in the Albian sample (FM 886) from Fetcham Mill. It was not present in the Turonian sample (FM 520). One specimen was observed in the North American material, in sample Sas 1084 (Albian) from Saskatchewan. Thus the known stratigraphic range is from Upper Aptian to Cenomanian.

Cyst-Family **EXOCHOSPHAERIDIACEAE** Sarjeant & Downie 1966

Genus ***EXOCHOSPHAERIDIUM*** Davey, Downie, Sarjeant & Williams 1966

REMARKS. *Exochosphaeridium* differs from *Trichodinium* Eisenack & Cookson (1960) in that the latter possesses a well developed cingulum.

Exochosphaeridium phragmites Davey, Downie, Sarjeant & Williams

(Pl. 7, fig. 5)

1966 *Exochosphaeridium phragmites* Davey, Downie, Sarjeant & Williams: 165, pl. 2, figs. 8–10.

DIMENSIONS. Range of observed specimens: maximum diameter of central body 41 (51·9) 67 μ, minimum diameter of central body 32 (46·7) 57 μ, maximum length of processes 10 (18·5) 40 μ. Number of specimens measured, 18.

REMARKS. Superficially *E. phragmites* resembles *E. striolatum* (Deflandre) which, however, has a definitely striated periphragm. *Trichodinium paucispinum* Eisenack & Cookson (1960) is also similar but has fewer processes and a well developed cingulum.

OCCURRENCE. *E. phragmites* is rare at most horizons throughout the Cenomanian of Fetcham Mill, Compton Bay and Escalles, and is recorded from the Albian sample, FM 886. It has not been recorded in the North American material.

Exochosphaeridium pseudohystrichodinium (Deflandre)

(Pl. 11, figs. 4, 5)

1937 *Hystrichosphaeridium pseudohystrichodinium* Deflandre : 73, pl. 15, figs. 3, 4.

1966 ?*Exochosphaeridium pseudohystrichodinium* (Deflandre); Davey, Downie, Sarjeant & Williams : 166.

1967 *Baltisphaeridium pseudohystrichodinium* (Deflandre); Clarke & Verdier: 75, pl. 15, fig. 7. (see also for earlier references).

EMENDED DIAGNOSIS. Shell spherical to ovoidal; shell wall thick, with pitted surface. Processes numerous, slightly fibrous, occasionally bifurcating medially, slender, broadening slightly proximally; distally truncated or terminated with small bifurcation. Cingular processes rarely aligned. Apical process sometimes branched and slightly larger than normal. Archaeopyle precingular, formed by loss of one or two plate areas.

HOLOTYPE. Slide AH. 55, Laboratoire de Micropaléontologie, École Practique des Hautes Études, Paris. (Figured by Deflandre 1937, pl. 15, fig. 3). Upper Cretaceous flint from the Paris Basin.

DIMENSIONS. Range of type material: shell length 49 to 54 μ, shell width 38 to 45 μ, overall length 80–90 μ. Range of observed specimens: diameter of central body 35 (43·8) 54 μ, maximum length of processes 13 (16·8) 21 μ. Number of specimens measured, 12.

DESCRIPTION. The shell wall is moderately thick (*c.* 1·5 μ), pitted (never striated), and bears a large number of broad-based processes. All the processes appear to be basically the same except for the apical process which is typically branched and is usually larger than normal.

The author was permitted, through the courtesy of Professor Deflandre, to make a detailed examination of the holotype and paratype. In the holotype the cingular processes were arranged in a definite circular manner around the shell. Such an alignment was not observed with certainty in any of the Cenomanian specimens studied. The archaeopyle, present in the paratype, is precingular and usually formed by the loss of two plate areas.

REMARKS. The Cenomanian specimens differ from the holotype only in that aligned circular processes were not observed. This may be due to unfavourable preservation or orientation of the specimens. The diagnosis of *E. pseudohystrichodinium* has been emended to include a description of the apical process and the archaeopyle.

The overall form of *E. pseudohystrichodinium* resembles species included in the " *hirsutum* " group, but the typical fibrous shell periphragm is absent. The formation of the archaeopyle by the loss of two precingular plates has also been observed in *E. striolatum* var. *truncatum* nov., indicating a relationship.

OCCURRENCE. This species is rather restricted, being common in samples FM 690, E 165 and E 159 and rare in samples FM 750, E 207 and FM 520 (Turonian). It appears, therefore, to be most common in the Upper Cenomanian. It was not recorded in the samples from North America. The recorded stratigraphic range is from Cenomanian to Eocene (Pastiels 1948).

Exochosphaeridium striolatum (Deflandre) comb. nov.

1937 *Hystrichosphaeridium striolatum* Deflandre : 72, pl. 15, figs. 1, 2.

DIAGNOSIS. Shell subspherical to ovoidal. Processes numerous, variable, fibrous, often bifurcate medially and sometimes terminating with small fork. Processes distally may be pointed or blunted. Fibres pass down length of processes onto shell surface and there join with similar fibres from adjacent processes. Apical process and precingular archaeopyle may be present.

HOLOTYPE. Slide AH. 89, Laboratoire de Micropaléontologie, École Practique des Hautes Études, Paris. (Figured by Deflandre 1937, pl. 15, fig. 1). Upper Cretaceous flint from the Paris Basin.

REMARKS. Through the courtesy of Professor Deflandre, I was able to examine the holotype and paratype of *E. striolatum*. On the holotype one process appeared to be unusually thick and may have been apical in position. Neither holotype nor paratype was observed to possess an archaeopyle but this may have been due to the fact that the lower surfaces of the specimens were extremely dark and could not be studied.

Exochosphaeridium striolatum (Deflandre) var. ***truncatum*** nov.

(Pl. 7, figs. 1–3)

DERIVATION OF NAME. Latin, *truncatus*, shorten by cutting off—with reference to the truncated extremities of the processes.

DIAGNOSIS. A variety of *E. striolatum* possessing subspherical to ovoidal shell; shell wall fibrous or lightly pitted. Processes numerous, typically fibrous and blunted distally, slender or subtriangular, rarely branched. Apical process large, often foliate. Precingular archaeopyle, commonly present, formed by loss of two plate areas, rarely one.

HOLOTYPE. B.M. (N.H.) V.51982 (1). Lower Chalk, Bureau de Recherches Géologiques et Minières Borehole, Escalles, Pas de Calais, at 159 metres depth. Upper Cretaceous (Cenomanian).

DIMENSIONS. Holotype: diameter of central body 66 by 67 μ, length of processes 17–22 μ. Range: diameter of central body 34 (56·1) 81 μ, maximum length of processes 6 (17·8) 27 μ. Number of specimens measured, 24.

DESCRIPTION. The shell possesses a moderately thick wall (*c.* 1 μ) but it is quite often distorted, especially when an archaeopyle is developed. The shell surface (periphragm) is typically fibrous; the fibres pass down the length of the processes onto the shell surface and, there, join up with similar fibres from adjacent processes. Some specimens are less conspicuously fibrous, the fibres being apparent near the bases of the processes and only extending a little way onto the shell surface. The remainder of the shell surface in these forms is lightly pitted. The processes may be fairly slender to subtriangular and are occasionally joined proximally. A small number of processes are subdivided medially. The processes are typically truncated distally but may be slightly bulbous. Process alignment was not observed.

The apical process is larger than the other processes and often foliate; the endophragm occasionally forms a small apical bulge beneath it. The archaeopyle is typically formed by the removal of two precingular plates, as is apparent by its shape. Rarely only one plate is lost. Detached opercula consisting of two precingular plates have been located (pl. 7, fig. 3).

REMARKS. *E. striolatum* var. *truncatum* nov. is a member of the "*hirsutum*" group, a group which is characterized by having fibres radiating from the bases of the processes over the shell surface. The truncate nature of the processes, although obvious, has not previously been remarked on. *Exochosphaeridium spinosum* var. *deflandrei* (Lejeuner-Carpentier 1941) is similar, the processes sometimes being bulbous distally, but they are very slender and appear never to be truncated. Two other forms, *E. striolatum* (Deflandre) (illustrated by Lejeune-Carpentier 1941 as *Hystrichosphaeridium hirsutum* text-figs. 1–4) and *E.* (*Hystrichosphaeridium*) cf. *hirsutum* (Cookson & Eisenack 1958), are also comparable, differing in that their processes are not truncated. *Baltisphaeridium bifidum* Clarke & Verdier (1967) is similar but possesses fewer and more slender processes which, however, are bifid distally. The above forms all belong to the "*hirsutum*" group and are rather similar, differing only in the detail form of the processes and perhaps in archaeopyle formation, which is noted here for the first time.

Although the precingular archaeopyle is typically, but not always, formed by the loss of two plate areas, this is not considered reason enough for the erection of a new genus. This species may indicate a trend towards the genus *Lingulodinium* Wall (1967) where four or five precingular plate areas are lost.

OCCURRENCE. *E. striolatum* var. *truncatum* is infrequent to fairly common at all horizons throughout the Cenomanian of Fetcham Mill, Compton Bay and Escalles.

At Fetcham Mill it has also been recorded from the Albian (sample FM 886) and Turonian (sample FM 520). A single specimen was obtained from the Upper Woodbine of Texas, but the species was absent from the Saskatchewan samples.

OTHER SPECIES

The following species and variety are here included in *Exochosphaeridium* on the basis of similarity in structure:

Exochosphaeridium spinosum (White 1842) comb. nov. 1842 *Xanthidium spinosum* White: Microsc. J., **11**, 35–40, pl. 4 fig. 6.

Exochosphaeridium spinosum var *deflandrei* (Lejeune-Carpentier 1941) comb. nov. 1941 *Hystrichosphaeridium spinosum* var. *defiandrei* Lejeune-Carpentier: Annls. Soc. géol. Belg., **63** (bull, 3), B84, figs. 6, 7.

Cyst-Family **AREOLIGERACEAE** Evitt emend. Sarjeant & Downie 1966

Genus ***CYCLONEPHELIUM*** Deflandre & Cookson emend. Williams & Downie 1966

Remarks. Four species are described from the Cenomanian, *C. distinctum* Cookson & Eisenack being the only one fairly common throughout this stage. *C. membraniphorum* Cookson & Eisenack, *C. vannophorum* sp. nov. and *C. paucispinum* sp. nov. are restricted in occurrence. One species *C. eisenacki* sp. nov., is described from the Albian of Saskatchewan. In the Cenomanian, the genus is most abundant at Escalles, rarest at Saskatchewan and absent from Texas, possibly indicating a preference for an open water environment.

Cyclonephelium distinctum Deflandre & Cookson

(Pl. 11, figs. 6–8, 10; Figs. 16 C, D, F)

1955 *Cyclonephelium distinctum* Deflandre & Cookson : 285, pl. 2, fig. 14.
1963 *Circulodinium deflandrei* Alberti, Balteş: 587, pl. 6, figs. 9–11.
1967 *Cyclonephelium distinctum* Deflandre & Cookson; Clarke & Verdier: 22, pl. 1, figs. 6, 7. (see also for earlier references).

Description. This species is extremely variable, as pointed out by Cookson & Eisenack (1962), and a member of most Cenomanian assemblages studied. The shell, which is always somewhat flattened, may be subcircular to ovoidal in outline and has a smooth or lightly granular shell wall. The regular outline is sometimes broken by an apical protuberance and more rarely by two reduced, antapical horns. The latter are of unequal size and when present the antapical region is slightly concave (Fig. 16F). The bald areas, typical of this genus, may occupy almost all of the ventral and dorsal surfaces of the shell leaving only the peripheral regions to bear processes, or may be practically invisible beneath the encroaching processes. Usually, however, these bald areas are circular to ovoidal in shape and occupy approximately thirty per cent of each side of the shell. The processes are usually abundant, extremely variable in form and typically under one-third of the shell width in length. They are solid and usually widen distally and proximally, may be fine or taeniate, and are often distally bifurcate. The bases of the processes are occasionally thickened and rarely a line of thickening on the shell surface joins one process with a neighbouring one. Equally rarely, and only when the processes are broad, they may be joined distally.

A large apical archaeopyle is always present. This is angular, possesses a pronounced zigzag margin and on the ventral surface usually a relatively deep sulcal notch. Although the archaeopyle is always discernible, the operculum is sometimes still attached. It then behaved as a lid, returning to its original position after the escape of the encysted organism.

DIMENSIONS. Range of observed specimens: height of shell (operculum absent) 41 (54·5) 82 μ, width 48 (61·8) 81 μ, maximum length of the processes 4 (10·7) 21 μ. Number of specimens measured, 50.

REMARKS. *C. distinctum* appears to be extremely variable, and specimens showing extremes in variation sometimes appear to be transitional to other species.

OCCURRENCE. Found throughout the Cenomanian of Fetcham Mill, Compton Bay and Escalles, and rare to common at all horizons. Two samples from Saskatchewan, samples Sas 890 and Sas 805, also contain *C. distinctum*. The species had a wide geographical distribution throughout most of the Cretaceous and is of little value in detailed stratigraphy.

Cyclonephelium membraniphorum Cookson & Eisenack

(Pl. 11, fig. 9)

1958 *Cyclonephelium compactum* Deflandre & Cookson : 48, pl. 12, fig. 8 only.
1962*b* *Cyclonephelium membraniphorum* Cookson & Eisenack : 495, pl. 6, figs. 8–14.
1964 *Cyclonephelium membraniphorum* Cookson & Eisenack; Cookson & Hughes : 44, pl. 10, figs. 5, 6.
1967 *Cyclonephelium membraniphorum* Cookson & Eisenack; Clarke & Verdier: 23, pl. 2, figs. 1, 2.

DESCRIPTION. The shell is always dorso-ventrally flattened, both the apex and antapex being circular to subcircular in outline. An apical archaeopyle is always developed, with a zigzag margin and sulcal notch. The bald areas, typical of this genus, may be relatively large or quite small and are surrounded by high membranes. The latter are braced by stout supports which arise from lines of thickening on the shell surface. These lines of thickened periphragm may be curved and may form semi-circular rings. When the latter are present, the membranes are in the form of wide tubular projections. The periphragm of the shell wall and the membranes is granular or pitted. The membranes may sometimes be fenestrate.

In some specimens attributed to *C. membraniphorum* the bald areas are practically non-existent. The membranes in these forms are particularly well developed and commonly are in the form of wide tubes or funnels. Distally they have a subcircular to polygonal outline and may possess a thickened outer rim bearing irregular pieces of periphragm (Pl. 11, fig. 9).

DIMENSIONS. Range of observed specimens: length of shell (operculum missing) 37 (50·6) 79 μ, width 41 (54·1) 82 μ, maximum height of membranes 6 (13·3) 26 μ. Number of specimens measured, 16.

Remarks. Many of the specimens observed appear identical with the Albian to Cenomanian forms from Australia, except that the former are considerably smaller, the largest of them only falling within the size range of the type material. It is not thought practical to separate the European forms solely on the size distinction and they have, therefore, been placed in the Australian species. An interesting variation is the apparent absence of the bald areas, although the overall shape and the apical archaeopyle typical of *Cyclonephelium* are present.

Occurrence. In addition to the Australian records, *C. membraniphorum* is rare and spasmodic throughout the Cenomanian of Fetcham Mill, Compton Bay and Escalles, though absent elsewhere. This species has also been recorded from the Turonian and Lower Senonian by Clarke & Verdier (1967).

Cyclonephelium vannophorum sp. nov.

(Pl. 9, fig. 3: Pl. 11, figs. 11, 12; Fig. 16E)

Derivation of name. Latin, *vannophorum*, fan-bearer—with reference to the fan-shaped processes.

Diagnosis. Shell subcircular in outline, with slight apical prominence and one or two reduced antapical horns. Shell wall coarsely granular with areas devoid of processes of moderate size. Processes numerous, short, solid, of irregular shape and often confluent distally. Apical archaeopyle with zigzag margin.

Holotype. B.M. (N.H.) slide V.51986 (1). Lower Chalk, Compton Bay, Isle of Wight at 15 feet 6 inches above the base of the Cenomanian. Upper Createceous (Cenomanian).

Dimensions. Holotype: length of shell (including operculum) 65 μ, width 62 μ, length of processes up to 8 μ. Range: length of shell (without operculum) 47 (57·8) 70 μ, width 56 (65·5) 78 μ, maximum length of processes 3 (5·3) 8 μ. Number of specimens measured, 11.

Description. When two antapical horns are present the portion of the shell between them is concave and from this region a broad furrow passes towards the apex. The furrow or sulcus decreases in width and depth in this direction and disappears just posterior to the archaeopyle margin. The processes vary greatly in size from mere enlarged granules (0·5 μ) to 8 μ in length. In the larger processes the stem is quite narrow, the distal third widening rapidly (Pl. 9, fig. 3) and is sometimes bifurcate. The processes are often joined to form a short line on the shell surface. Rarely the cingulum is just discernible by a concentration of small processes along its borders.

Remarks. *C. vannophorum* sp. nov. is most closely comparable to ?*C. attadalicum* Cookson & Eisenack (1962*b*) from the Aptian/Albian of Australia. The processes are similar in form but the shell of ?*C. attadalicum* is more polygonal and the cingulum is always well defined.

Occurrence. *C. vannophorum* has only been recorded from the Lower Cenomanian sample CB 3 (Compton Bay) and it there comprises about 2% of the micro-

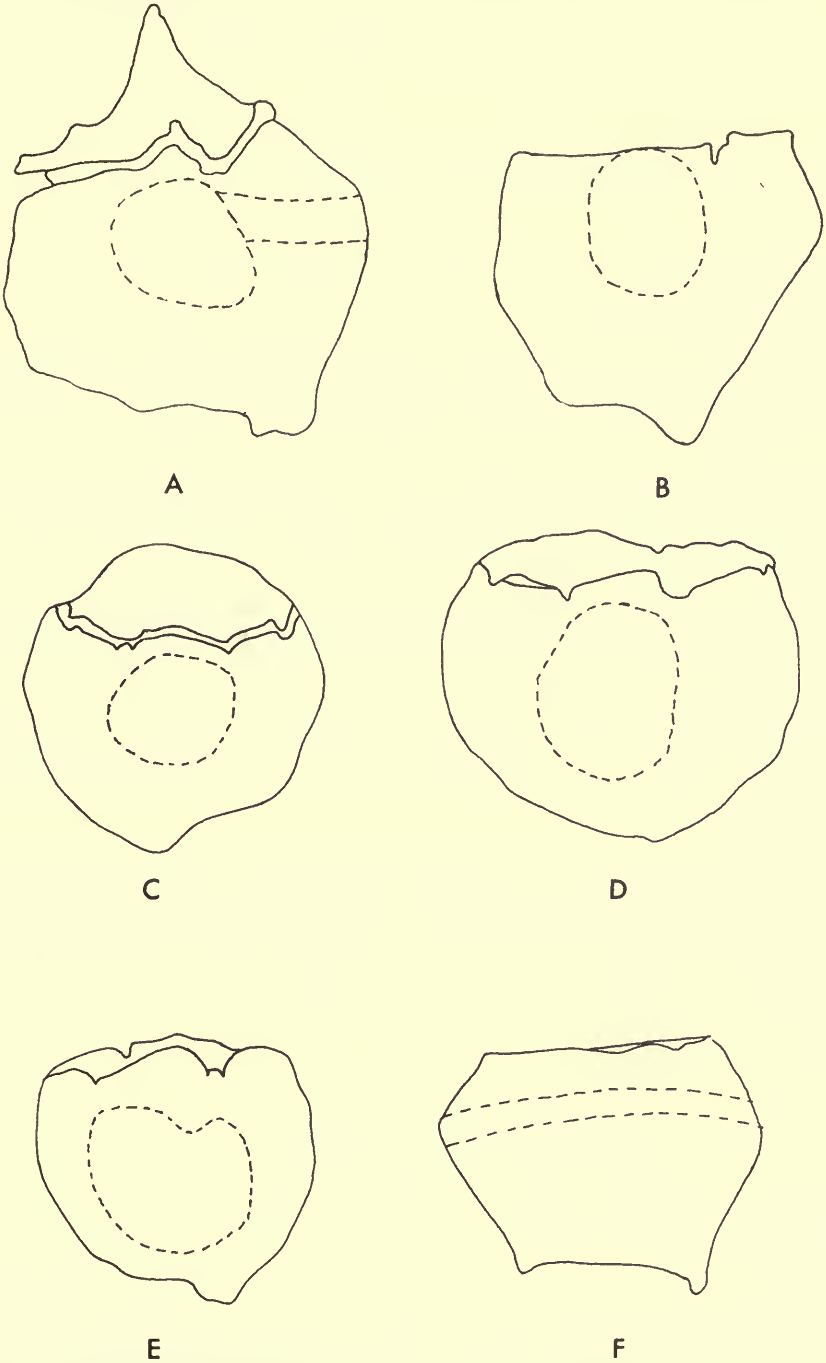

FIG. 16. *Cyclonephelium eisenacki* sp. nov., A. Complete specimen (× 700). B. Specimen illustrating apical archaeopyle (× 700). *Cyclonephelium distinctum* Deflandre & Cookson, C. D. and F. Illustrating variation in the shape of the shell of this species (processes removed) (× 700). *Cyclonephelium vannophorum* sp. nov., E. Specimen with well developed apical archaeopyle (processes removed) (× 700).

plankton content. The unusual distribution and the similarity to a Lower Cretaceous species indicate that *C. vannophorum* is possibly a derived form.

Cyclonephelium paucispinum sp. nov.

(Pl. 9, figs. 1, 2)

Derivation of name. Latin, *paucus*, few; *spina*, thorn—with reference to the scarcity of the processes.

Diagnosis. Shell subpolygonal in outline with well defined antapical horn. Shell wall lightly to coarsely granular, bearing small number of irregularly distributed processes confined to peripheral region of shell. Processes of moderate size, solid and widening distally. Apical archaeopyle with a zigzag margin and sulcal notch.

Holotype. B.M. (N.H.) V.51981 (2). Lower Chalk, Bureau de Recherches Géologiques et Minières Borehole, Escalles, Pas de Calais at 165 metres depth. Upper Cretaceous (Cenomanian).

Dimensions. Holotype: length of shell (operculum missing) 54 μ, width 81 μ, length of processes 1·5–12 μ. Range: length of shell (operculum missing) 40 (72·4) 92 μ, width 54 (87·0) 112 μ, maximum length of processes 5 (10·2) 19 μ. Number of specimens measured, 12.

Description. The shell is subpolygonal in outline, the cingular region being the widest portion of the shell. Posteriorly there is a pointed antapical horn. The few processes present are of moderate size and if close together tend to anastomose both distally and proximally.

Remarks. The large size, the paucity of processes and the subpolygonal shape of the shell distinguish *C. paucispinum* sp. nov. from all previously described species. The processes most closely resemble those of *C. distinctum* but are fewer in number.

Occurrence. *C. paucispinum* is rare in samples E 165, CB 3, and common in sample CB 11. The distribution is, therefore, rather erratic in the Lower, Middle and Upper Cenomanian.

Cyclonephelium eisenacki sp. nov.

(Pl. 8, figs. 3, 4; Pl. 9, fig. 4; Figs. 17A, B)

1960 *Aptea cf. polymorpha* Eisenack & Cookson : **9**, Pl. 3, figs. 2–4.

Derivation of name. The species is named after Professor A. Eisenack.

Diagnosis. Shell subtriangular, flattened, with convex sides. Apical horn well developed; antapical horns, if present, very reduced. Greater part of shell surface ornamented by complex network of low crests and short, capitate processes. In centre of both dorsal and ventral sides there is a circular area devoid of ornamentation. Apical archaeopyle always present.

HOLOTYPE. B.M. (N.H.) V. 51980(2). Upper Lower Colorado (Fish Scale Zone?), International Yarbo Borehole No. 17, Saskatchewan at 1023 feet depth. Lower Cretaceous (Albian).

DIMENSIONS. Holotype: shell length 70 μ, width 66 μ, height of crests 1–5 μ. Range: shell length 70–92 μ (4 complete specimens measured); shell length (operculum missing) 55 (63·1) 71 μ, width 66 (72·1) 84 μ, height of crests 2 (4·2) 7 μ. Number of specimens measured, 12.

DESCRIPTION. The shell surface is ornamented by a very characteristic network of low crests or lamellae which are often broken, so forming isolated processes. A poorly-marked cingulum, outlined by the crests, is occasionally discernible. The apical operculum is often in position.

REMARKS. The illustrations of *Aptea* cf. *polymorpha* indicate that these specimens belong in the genus *Cyclonephelium* and may well be conspecific with the Canadian specimens here described. This species differs from *Aptea polymorpha* Eisenack (1958) by the absence of the numerous fine processes and the outer membranous structure which they support. *Pseudoceratium turneri* Cookson & Eiesnack (1958), from the Aptian/Albian of Australia, possesses a similar but stronger ornamentation. Also the apical and antapical horns are usually much better developed, although the specimen of *P. turneri* illustrated (*loc. cit.* pl. 5, fig. 5), approaches a number of the *C. eisenacki* examples.

OCCURRENCE. *C. eisenacki* sp. nov. is fairly common in two samples from Saskatchewan, samples Sas 1084 and 1023. It has not been recorded elsewhere in the material examined.

Cyst-Family **ADNATOSPHAERIDIACEAE** Sarjeant & Downie 1966

Genus ***ADNATOSPHAERIDIUM*** Williams & Downie 1966

Adnatosphaeridium chonetum (Cookson & Eisenack) comb. nov.

(Pl. 10, figs. 11, 12.)

1962*b* ?*Cannosphaeropsis choneta* Cookson & Eisenack : 493, pl. 4, figs. 8–10.

DESCRIPTION. The shell is spherical to subspherical and bears a number of more or less tubular processes which possess bands of thickening for support. The processes are usually joined to their neighbour either along their entire length, or only distally by membranes. However, isolated tubular processes are occasionally visible. The impression obtained from most specimens is of a complex membranous network perpendicular to the shell surface. A well developed apical archaeopyle is typically present.

DIMENSIONS. Range of observed specimens: shell diameter 27 (34·1) 46 μ, length of processes 6 (10·4) 24 μ. Number of specimens measured, 15.

REMARKS. The Cenomanian specimens examined strongly resemble, but are slightly smaller than, the type material from the Cenomanian of Australia. This species, tentatively placed in *Cannosphaeropsis* by Cookson & Eisenack, is here transferred to *Adnatosphaeridium* because of the presence of interconnecting processes and an apical archaeopyle.

OCCURRENCE. Apart from the Australian occurrence, it is infrequent to common in the Middle and Upper Cenomanian of Fetcham Mill and Escalles, not occurring below samples FM 790 and E 195. Only one specimen was recorded from Compton Bay, in sample CB 19.

Cyst-Family **HYSTRICHOSPAERACEAE** O. Wetzel emend. Sarjeant & Downie 1966

Genus ***HYSTRICHOSPHAERA*** O. Wetzel emend. Davey & Williams 1966

Hystrichosphaera ramosa var. ***ramosa*** (Ehrenberg)

(Pl. 10, figs. 1, 2, 5)

1838 *Xanthidium ramosum* Ehr.: pl. 1, figs. 1, 2, 5.
1966*a* *Hystrichosphaera ramosa* (Ehr.) var. *ramosa* Davey & Williams : 33, pl. 1, figs. 1, 6; pl. 3, fig. 1; text-fig. 8. (See also for earlier references).
1967 *Hystrichosphaera furcata* (Ehr.) Clarke & Verdier: 48, pl. 8, figs. 12, 13.

DIMENSIONS. Range of observed specimens: diameter of central body 29 (40·7) 56 μ, maximum length of processes 13 (19·8) 27 μ. Number of specimens measured, 32.

OCCURRENCE. This variety has a known stratigraphic range from the Oxfordian (Jurassic) to the Ypresian (Eocene). It is a common variety throughout the Cenomanian of Fetcham Mill, Compton Bay and Escalles, and is rare to infrequent in the material from Saskatchewan and Texas.

Hystrichosphaera ramosa (Ehrenberg) var. ***gracilis*** Davey & Williams

1955 *Hystrichosphaera ramosa* (Ehr.) Deflandre & Cookson : 263, pl. 5, fig. 8.
1963 *Hystrichosphaera ramosa* (Ehr.) Górka : 48, pl. 6, figs. 6, 7.
1966*a* *Hystrichosphaera ramosa* (Ehr.) var. *gracilis* Davey & Williams : 34, pl. 1, fig. 5; pl. 5, fig. 6.

DIMENSIONS. Range of observed specimens: diameter of central body 28–35 μ, maximum length of processes 16–22 μ. Number of specimens measured, 5.

OCCURRENCE. The known stratigraphic range of this variety is from the Cenomanian (England) to the Miocene (Australia). It is rare to infrequent at most horizons throughout the Cenomanian of Fetcham Mill, Compton Bay and Escalles, but has not been recorded in the North American material.

Hystrichosphaera ramosa (Ehrenberg) var. ***multibrevis*** Davey & Williams

(Pl. 10, figs. 3, 4)

1955 *Hystrichosphaera furcata* (Ehr.) Valensi : 586, pl. 4, fig. 4; pl. 5, fig. 12.
1958 *Hystrichosphaera furcata* (Ehr.) Eisenack : 406, pl. 25, figs. 4–8.
1966*a Hystrichosphaera ramosa* (Ehr.) var. *multibrevis* Davey & Williams : 35, pl. 1, fig. 4; pl. 4, fig. 6; text-fig. 9.

DIMENSIONS. Range of observed specimens: diameter of central body 31 (39·7) 51 μ, maximum length of processes 10 (14·3) 21 μ. Number of specimens measured, 13.

OCCURRENCE. *H. ramosa* var. *multibrevis* has a stratigraphic range from the Lower Cretaceous (Hauterivian) to the Eocene (Ypresian). It is rare to infrequent in all samples examined from Fetcham Mill, Compton Bay and Escalles. It has also been recorded from the Lower Cretaceous (Albian) of Saskatchewan, in samples Sas 967, 1023 and 1084.

Hystrichosphaera ramosa (Ehrenberg) var. ***reticulata*** Davey & Williams

1966*a Hystrichosphaera ramosa* (Ehr.) var. *reticulata* Davey & Williams : 38, pl. 1, fig. 2.

DIMENSIONS. Range of observed specimens: diameter of central body 33 (45·2) 59 μ, maximum length of processes 13 (15·3) 17 μ. Number of specimens measured, 13.

OCCURRENCE. This variety is rare to infrequent at most horizons throughout the Cenomanian of Fetcham Mill, Compton Bay and Escalles. It has also been recorded in two Albian samples from Saskatchewan, samples Sas 967 and 1084.

Hystrichosphaera cingulata var. ***cingulata*** (O. Wetzel)

1933 *Cymatiosphaera cingulata* O. Wetzel : 28, pl. 4, fig. 10.
1966*a Hystrichosphaera cingulata* (O. Wetzel) Davey & Williams : 38, pl. 1, fig. 9. (See also for earlier references).
1967 *Hystrichosphaera cingulata* var. *cingulata* (O. Wetzel) Clarke & Verdier: 45, pl. 8, figs. 9, 10.

DIMENSIONS. Range of observed specimens: diameter of central body 26 (36·8) 48 μ, maximum height of crests 5 (7·0) 13 μ. Number of specimens measured, 16.

OCCURRENCE. *H. cingulata* is infrequent at all horizons throughout the Cenomanian of Fetcham Mill, Compton Bay and Escalles. It has not been observed in the North American material. The recorded stratigraphic range is from Albian to Middle Miocene.

Hystrichosphaera cingulata (O. Wetzel) var. ***reticulata*** Davey & Williams

1966*a Hystrichosphaera cingulata* var. *reticulata* Davey & Williams : 39, pl. 1, fig. 10; pl. 2, fig. 4.
1967 *Hystrichosphaera cingulata* var. *perforata* Clarke & Verdier : 46, pl. 9, figs. 2–4, text-fig. 19.

DIMENSIONS. Range of observed specimens: diameter of central body 33 (42·8) 59 μ, maximum height of crests 7 (10·2) 17 μ. Number of specimens measured, 14.

OCCURRENCE. *H. cingulata* var. *reticulata* is rare to infrequent throughout the Cenomanian of Fetcham Mill, Compton Bay and Escalles. It appears to be slightly more common in the Middle and Upper Cenomanian at these localities. It has not been observed in the North American samples. Clarke & Verdier (1967) also record this variety from the Turonian and Senonian.

Hystrichosphaera crassimurata Davey & Williams

1966*a* *Hystrichosphaera crassimurata* Davey & Williams : 39, pl. 1, fig. 11.
1967 *Hystrichosphaera cingulata* var. *polygonalis* Clarke & Verdier: 47, pl. 8 figs. 7, 8, text-fig. 20.

DIMENSIONS. Range of observed specimens: diameter of central body 36–46 μ, height of crests, up to 14 μ. Number of specimens measured, 4.

OCCURRENCE. *H. crassimurata* is very rare to rare in the Middle and Upper Cenomanian of Fetcham Mill, Compton Bay and Escalles, the lowest samples in which it is found being FM 790, E 195 and CB 9. It has also been recorded from the Upper Woodbine Formation of Texas but is absent from the Saskatchewan material.

Hystrichosphaera crassipellis Deflandre & Cookson

1954 *Hystrichosphaera crassipellis* Deflandre & Cookson: text-fig. 5.
1966*a* *Hystrichosphaera crassipellis* Deflandre & Cookson; Davey & Williams : 40, pl. 1, figs. 7, 8. (See also for earlier references).
1967 *Hystrichosphaera crassipellis* Deflandre & Cookson; Clarke & Verdier: 48, pl. 8, fig. 11; pl. 9, fig. 1.

DIMENSIONS. Range of observed specimens: diameter of central body 34 (47·9) 68 μ, maximum length of processes 10 (17·8) 29 μ. Number of specimens measured, 19.

OCCURRENCE. *H. crassipellis* is rare at most horizons throughout the Cenomanian of Fetcham Mill, Compton Bay and Escalles; it has not been recorded in the North American material. The recorded stratigraphic range is from Cenomanian to Middle Miocene (Gerlach 1961).

Genus ***ACHOMOSPHAERA*** Evitt 1963

Achomosphaera ramulifera (Deflandre)

(Pl. 10, fig. 7)

1935 *Hystrichosphaera* cf. *ramosa* (Ehr.) Deflandre : pl. 5, fig. 11.
1966*a* *Achomosphaera ramulifera* (Deflandre) Davey & Williams : 49, pl. 2, fig. 3. (See also for earlier references).
1967 *Achomosphaera ramulifera* (Deflandre); Clarke & Verdier: 40, pl. 8, fig. 1.

DIMENSIONS. Range of observed specimens: diameter of central body 36 (44·7) 61 μ, maximum length of processes 16 (25·8) 36 μ. Number of specimens measured, 14.

Occurrence. This species has a known stratigraphic range from the Cenomanian to the Eocene (Pastiels 1948). It is a very rare to infrequent species at most horizons in the Cenomanian from Fetcham Mill, Compton Bay and Escalles. It is absent from the North American samples.

Achomosphaera sagena Davey & Williams

1966*a* *Achomosphaera sagena* Davey & Williams : 31, pl. 2, figs. 1, 2.
1967 *Achomosphaera reticulata* Clarke & Verdier: 41, pl. 8, figs. 2, 3, text-fig. 16.

Dimensions. Range of type material: diameter of central body 35 (48·4) 59 μ, maximum length of processes 17 (20·8) 28 μ. Number of specimens measured, 12.

Occurrence. *A. sagena* is a very rare to rare species occurring spasmodically in the Cenomanian samples from Fetcham Mill, Compton Bay and Escalles. Clarke & Verdier (1967) have also recorded it (as *A. reticulata*) from the Turonian and Senonian.

Genus ***Hystrichodinium*** Deflandre emend. Clarke & Verdier 1967

Hystrichodinium voigti (Alberti)

(Pl. 10, figs. 6, 10)

1961 *Heliodinium voigti* Alberti : 33, pl. 8, figs. 1–5.
1966*a* *Heliodinium voigti* Alberti; Sarjeant : 142, pl. 16, fig. 2; text-fig. 36.
1967 *Hystrichodinium voigti* (Alberti) Clarke & Verdier: 38.

Description. The shell is ovoidal to subpolygonal. The periphragm is smooth or slightly granular, and forms sutural crests and ribbon-like processes. The former are variably developed, may occasionally be absent, but when present give rise to long, flexuous processes along their length. When the crests are absent the processes arise directly from the shell surface. The processes are not confined to the plate boundaries and may be distributed at random over the shell surface. The processes are thin-walled, typically simple and occasionally terminate with bifurcate or trifurcate extremities. The cingulum (4–5 μ wide) is always delimited by low crests and is strongly helicoid. A precingular archaeopyle, formed by the loss of plate 3″, is typically present. One detached operculum has been located and bears five processes.

Dimensions. Range of observed specimens: shell length 40 (49·6) 62 μ, width 40 (48·4) 58 μ, length of processes 27 (35·6) 48 μ. Number of specimens measured, 11.

Occurrence. *H. voigti* is rare to fairly common and found spasmodically throughout the Cenomanian of Fetcham Mill, Compton Bay and Escalles. It was originally described by Alberti (1961) from the Lower Barremian to ?Lower Aptian of Germany. The specimens described by Sarjeant (1966*a*) are from the Cenomanian of Fetcham Mill.

Hystrichodinium dasys sp. nov.

(Pl. 10, figs. 8, 9)

Derivation of name. Latin, *dasys*, hairy or shaggy—with reference to the abundant hair-like processes.

DIAGNOSIS. Shell subspherical, thin-walled, smooth or slightly granular. Tabulation very faintly marked; cingulum, and more rarely, precingular and postcingular plate boundaries visible. Processes numerous, short, fine and flexuous, aligned along plate boundaries, also intratabular. Archaeopyle not observed.

HOLOTYPE. B.M. (N.H.) V.51982 (3). Lower Chalk, Bureau de Recherches Géologiques et Minières Borehole, Escalles, Pas de Calais at 159 metres depth. Upper Cretaceous (Cenomanian).

DIMENSIONS. Holotype: diameter of central body 58 by 61 μ, length of processes 10–14 μ. Range: diameter of central body 42 (53·0) 70 μ, maximum length of processes 7 (10·6) 14 μ. Number of specimens measured, 13.

DESCRIPTION. The shell, being thin-walled, is always found deformed. Only two specimens possess a faint tabulation. This is best seen in the holotype which has a clear but lightly defined cingulum and two or three precingular and postcingular plate boundaries visible. The numerous processes are hair-like, approximately 0·2 μ wide for most of their length, probably hollow and terminate with a point. The most characteristic feature of the processes is their extreme flexibility.

REMARKS. The characteristic processes and the presence of a tabulation differentiate *H. dasys* sp. nov. very easily from all previously described microplankton species.

OCCURRENCE. This species is rare to common in all samples from Escalles except the lower three (E 201, E 207, and E 213). One specimen was recorded from Compton Bay (sample CB 7) and two from Fetcham Mill (sample FM 520, Turonian). The species was not recorded from the North American material. The distribution of *H. dasys* possibly indicates an environmental difference between Escalles and Fetcham Mill/Compton Bay, perhaps in the depth of water or distance from land.

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PLATE 1

Gonyaulacysta exilicristata sp. nov.

Fetcham Mill Borehole (depth, 730 feet).

FIG. 1. Dorsal surface of holotype. Slide PF. 3987 (1). × 500.
FIG. 2. Ventral surface. Slide PF. 3987. × 500.

Carpodinium obliquicostatum Cookson & Hughes

FIG. 3. Lower Chalk, Fetcham Mill Borehole (depth, 750 feet). Lateral view. Slide PF. 3988. × 500.

FIG. 4. Lower Chalk, Escalles Borehole (depth, 159 metres). Dorsal surface with archaeopyle. Slide E 195/3. × 1250

Histocysta palla sp. nov.

Fetcham Mill Borehole.

FIG 5. Holotype; view of archaeopyle and attached operculum. Slide PF. 3052. × 500.
FIG. 6. Paratype; Antapical view. Slide PF. 3991 (1). × 500.

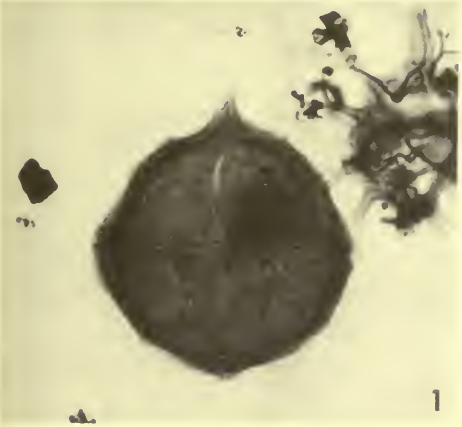
Gonyaulacysta delicata sp. nov.

FIG. 7. Ventral surface of holotype. V. 51979 (1). × 500.
FIG. 8. Paratype; V. 51979(2). × 500.

Gonyaulacysta sp. A. Figured specimen.

Lower Chalk, Fetcham Mill Borehole.

FIG. 9. Ventral surface. Slide PF. 3987 (2). × 500
FIG 10. Medial view. Slide PF. 3987 (2). × 500.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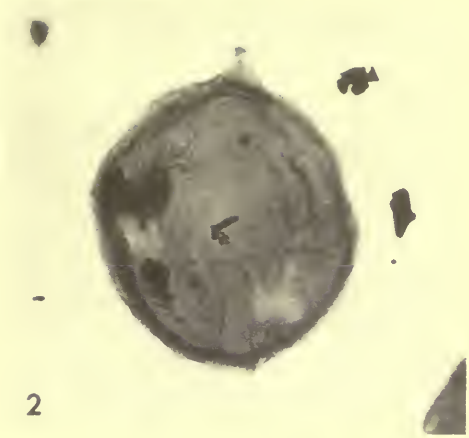
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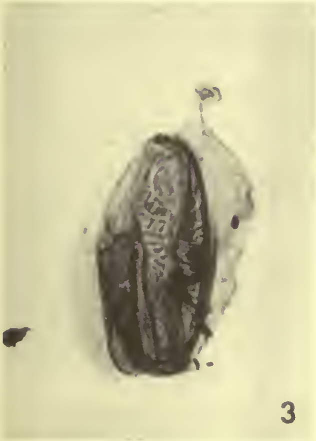
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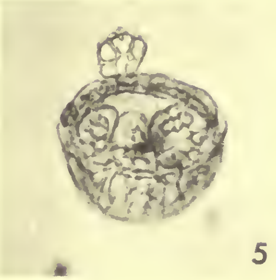
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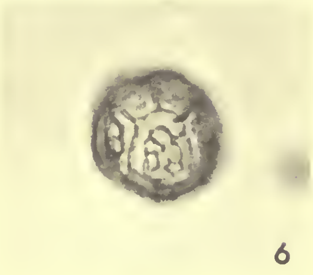
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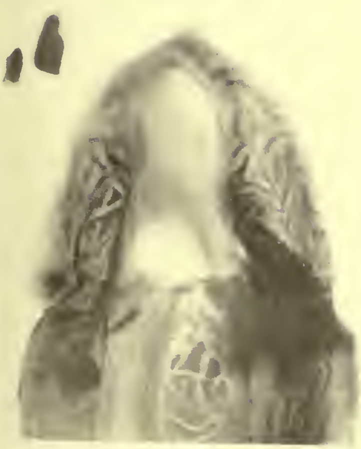

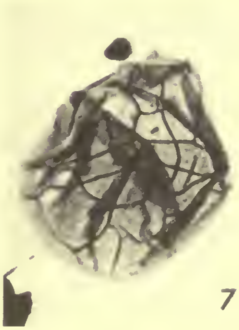
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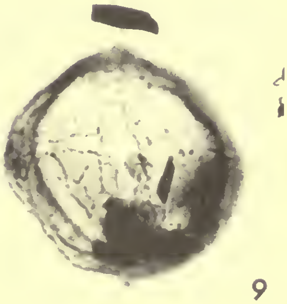
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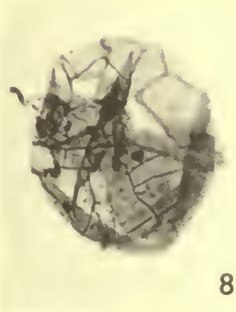
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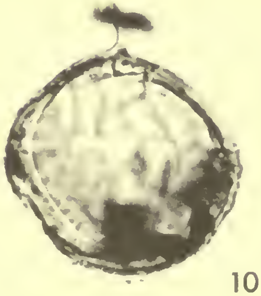
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PLATE 2

Cribroperidinium intricatum sp. nov.

FIG. 1. Ventral surface of holotype. V. 51980 (1). × 500.

FIG. 2. Lower Colorado, Saskatchewan (depth, 1,023 feet). Dorsal surface with operculum *in situ.* V.51980. × 500.

FIG. 3. Lower Colorado, Saskatchewan. Detached operculum. Slide Sas 1023/3. × 500.

Microdinium setosum Sarjeant.

FIG. 4. Lower Chalk, Fetcham Mill Borehole (depth, 840 feet). Lateral view. Slide PF. 3036. × 640.

Microdinium variospinum sp. nov.

FIG. 5. Lower Chalk, Escalles Borehole (depth, 195 metres). Antapical sutural spines visible. Slide E 195/3. × 640.

FIG. 6. Lateral view of holotype. V. 51981 (1). × 640.

?***Microdinium crinitum*** sp. nov.

FIG. 7. Lower Chalk, Fetcham Mill Borehole (depth, 770 feet). Slide FM 770/15. × 640.

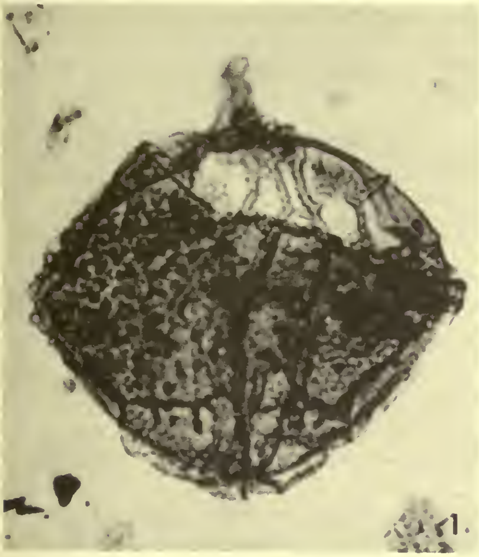
FIG. 8. Dorsal surface of holotype Slide PF. 3990 (1). × 640.

Microdinium distinctum sp. nov.

FIG. 9. Ventral surface of holotype. Slide PF. 3989 (1). × 640.

FIG. 10. Dorsal surface of holotype. × 640.

FIG. 11. Lower Chalk, Fetcham Mill Borehole (depth, 790 feet). Ventral surface. Slide FM 790/16. × 640.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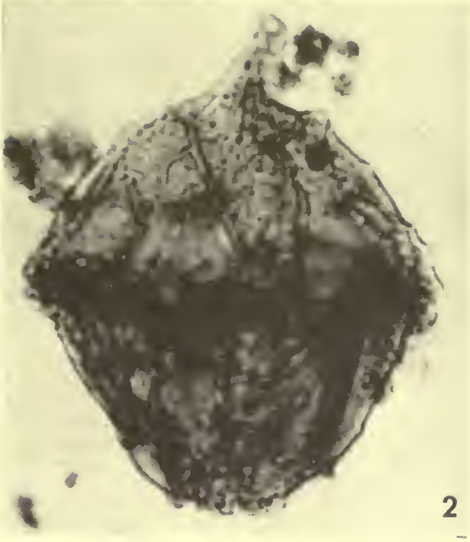
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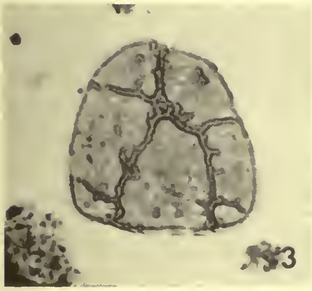
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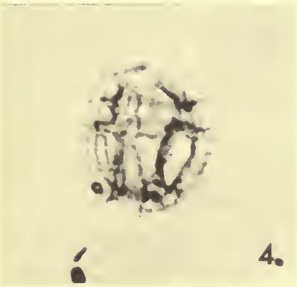
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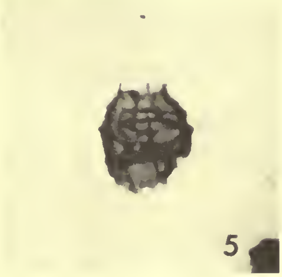
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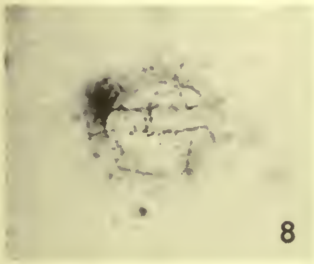
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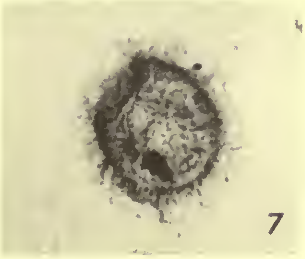
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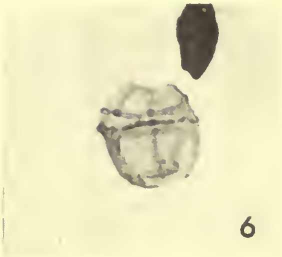
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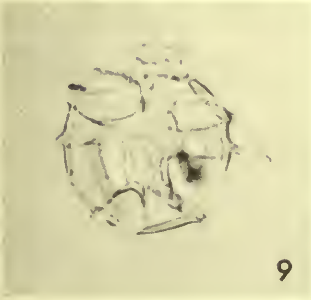
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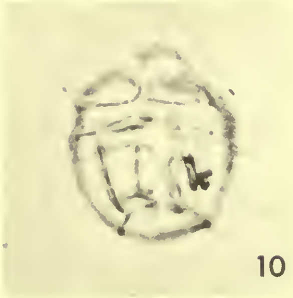
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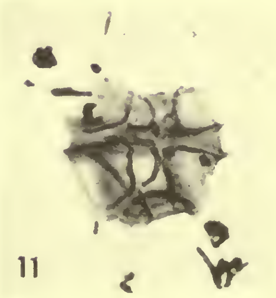
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PLATE 3

Ellipsodinium rugulosum Clarke & Verdier

FIG. 1. Lateral view of specimen showing operculum partially detached. Slide PF. 3988. × 1250.

Fromea amphora Cookson & Eisenack

Lower Chalk, Fetcham Mill Borehole.

FIG. 2. Slide FM 770/6 (depth, 770 feet). × 500.
FIG. 3. Specimen with operculum attached (depth, 650 feet). Slide PF. 3041. × 500.

Microdinium veligerum (Deflandre).

FIG. 4. Lower Chalk, Fetcham Mill Borehole (depth, 650 feet). Antapical view to show crestal cavities. Slide FM 650/5. × 1250.

Apteodinium granulatum Eisenack.

FIG. 5. Lower Chalk, Fetcham Mill Borehole (depth, 690 feet). Ventral surface. Slide FM 690/12. × 640.
FIG. 6. Lower Chalk, Escalles Borehole (depth, 165 metres). Lateral view. V. 51981. × 640.

Cassiculosphaeridia reticulata sp. nov.

FIG. 7. Lower Chalk, Fetcham Mill Borehole (depth, 730 feet). Operculum partially detached. Slide FM 730/9. × 500.

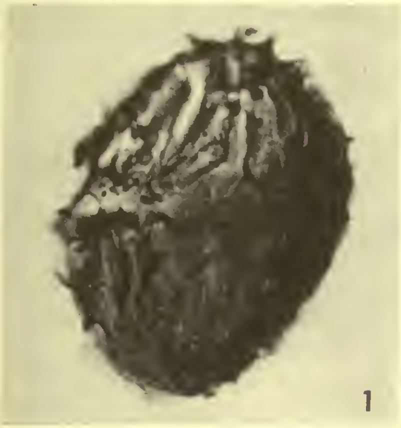
Chytroeisphaeridia euteiches sp. nov.

FIG. 8. Holotype showing archaeopyle. V. 51982 (2). × 500.
FIG. 9. Lower Chalk, Escalles Borehole (depth, 159 metres). Archaeopyle with detached operculum. V. 51982. × 500.

Epelidosphaeridia spinosa (Cookson & Hughes)

Lower Chalk, Fetcham Mill Borehole.

FIG. 10. Dorsal surface. Slide PF. 3992, (depth, 770 feet). × 500.
FIG. 11. Ventral surface with sulcus. Slide PF. 3992 (depth, 770 feet). × 500.
FIG. 12. Complete specimen. Slide PF. 3048 (depth, 770 feet). × 500.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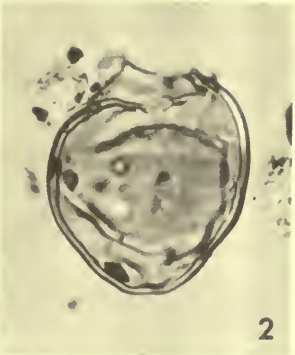
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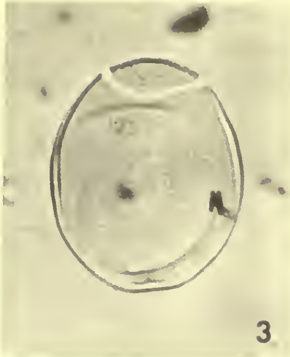
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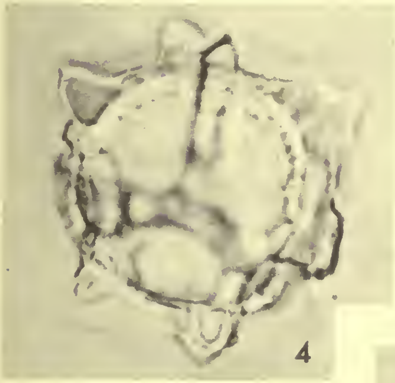
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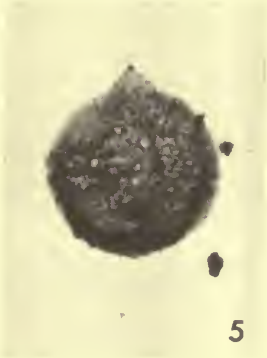
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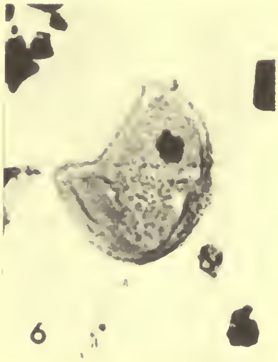
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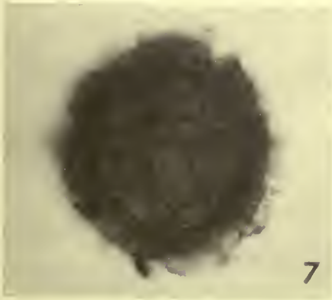
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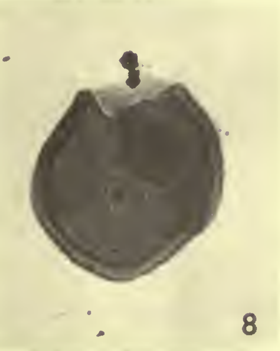
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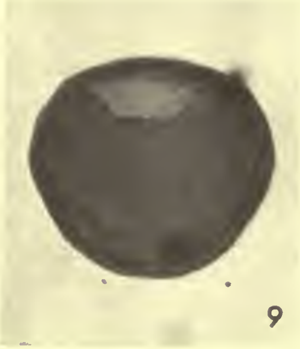
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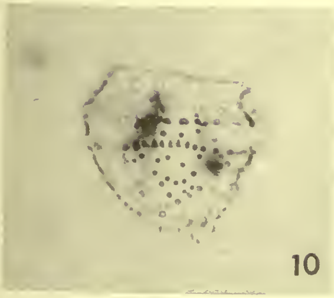
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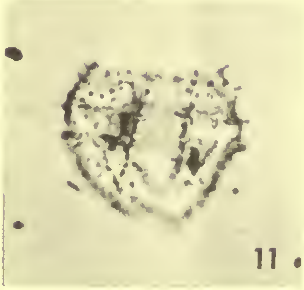
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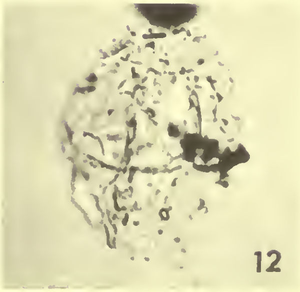
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PLATE 4

Hystrichosphaeridium deanei Davey & Williams

FIG. 1. Lower Chalk, Compton Bay. Complete specimen (137 feet above base of Chalk). Slide CB 19/2. × 500.

Hystrichosphaeridium difficile Manum & Cookson

Upper Colorado, Saskatchewan.

FIG. 2. Complete specimen, archaeopyle partially detached. V.51983 (depth, 805 feet). × 500.

FIG. 6. Detached operculum bearing 4 processes. Slide Sas 805/3 (depth, 805 feet). × 500.

FIG. 7. Detached operculum, lateral view. Slide Sas 805/3 (depth, 805 feet). × 500. × 500.

Cassiculosphaeridia reticulata sp. nov.

FIG. 3. Holotype; view of archaeopyle. V. 51981 (4). × 500.

Microdinium veligerum (Deflandre).

FIG. 4. Lower Chalk, Fetcham Mill Borehole (depth, 750 feet). Dorsal surface. Slide PF. 3988. × 640.

Microdinium cf. **ornatum** Cookson & Eisenack

FIG. 5. Lower Chalk, Escalles Borehole (depth, 189 metres). Dorsal surface. Slide E 189/4. × 640.

Hystrichosphaeridium radiculatum Davey & Williams

FIG. 8. Lower Chalk, Escalles Borehole (depth, 159 metres). Lateral view showing archaeopyle. V. 51982. × 500.

Hystrichosphaeridium mantelli Davey & Williams.

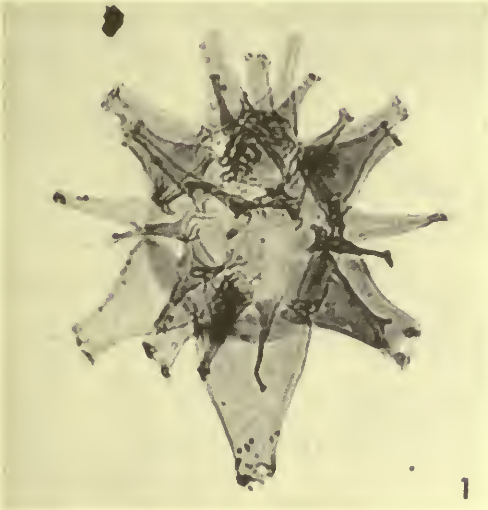
FIG. 9. Lower Chalk, Escalles Borehole (depth, 153 metres). Lateral view to show archaeopyle. Slide E 153/3. × 500.

Polysphaeridium laminaspinosum Davey & Williams

Lower Chalk, Fetcham Mill Borehole.

FIG. 10. Apical view showing archaeopyle. Slide PF. 3035 (depth, 840 feet). × 500.

FIG. 11. Antapical view. Slide PF. 3035 (depth, 840 feet). × 500.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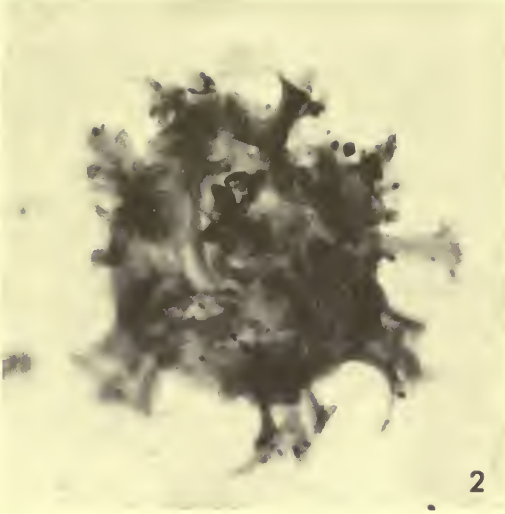
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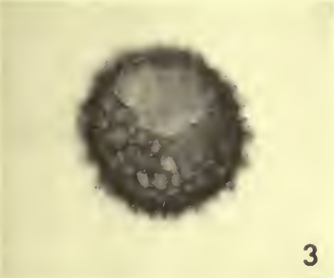
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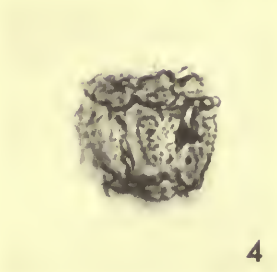
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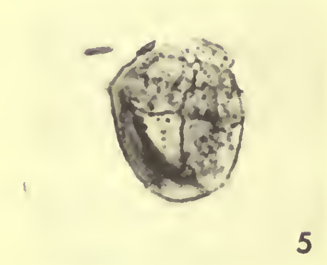
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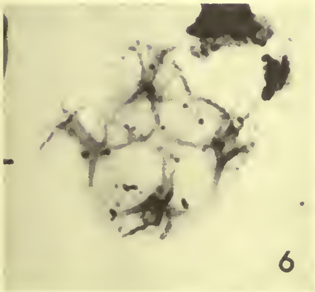
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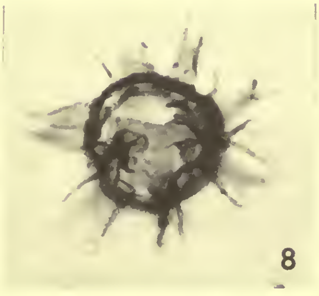
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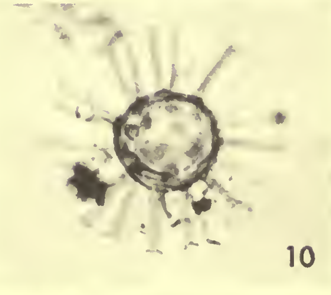
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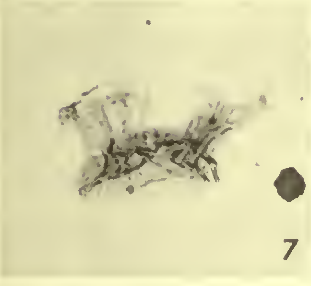
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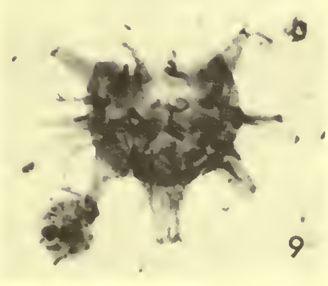
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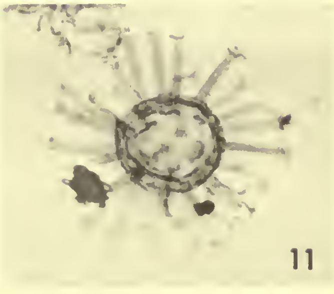
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PLATE 5

Oligosphaeridium anthophorum (Cookson & Eisenack)

Lower Colorado, Saskatchewan.

Fig. 1. Enlargement to show process extremities. Slide Sas 1023/3 (depth, 1023 feet). × 975.

Fig. 2. Detached operculum. Slide Sas 1023/1 (depth, 1023 feet). × 500.

Fig. 3. V. 51980 (boring depth, 1023 feet). × 500.

Oligosphaeridium prolixispinosum Davey & Williams

Fig. 4. Lower Chalk, Compton Bay (116 feet above the base of the Chalk). Specimen showing " bald " cingular region. Slide CB 17/C. × 500.

Hystrichosphaeridium tubiferum (Ehrenberg)

Lower Chalk, Fetcham Mill Borehole.

Fig. 5. Detached operculum. Slide FM 690/12 (depth, 690 feet). × 500.

Fig. 8. Slide PF. 3987 (depth, 730 feet). × 500.

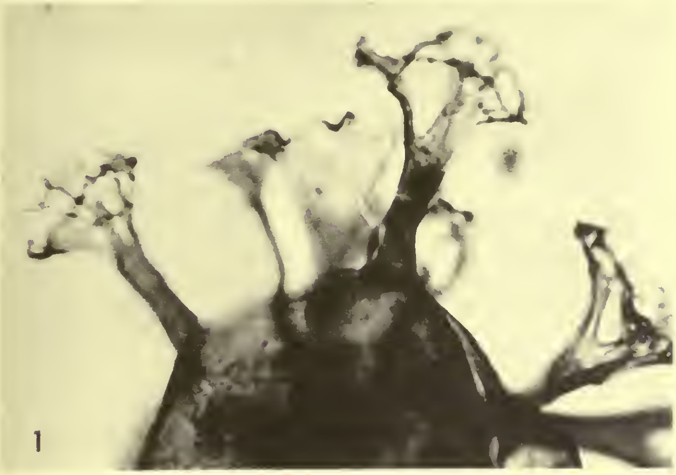
Oligosphaeridium complex (White)

Fig. 6. Lower Chalk, Escalles Borehole (depth, 159 metres). Detached operculum composed of 4 plates. V. 51982. × 500.

Fig. 7. Lower Chalk, Fetcham Mill Borehole (depth, 750 feet). Specimen illustrating the 6 precingular processes. Slide FM 750/13. × 500.

Hystrichosphaeridium bowerbanki Davey & Williams

Fig. 9. Lower Chalk, Compton Bay (116 feet above the base of the Chalk). Lateral view, archaeopyle to the north. Slide CB 17/C. × 500.



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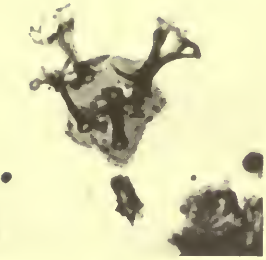

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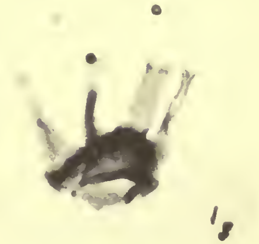

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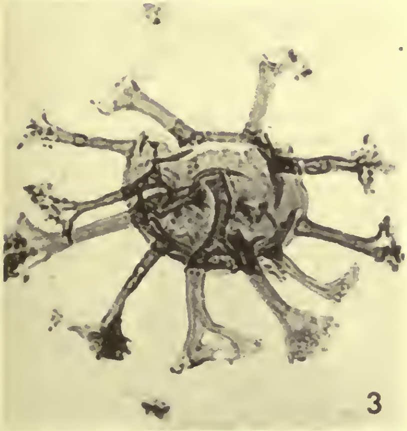

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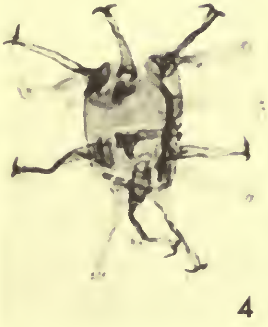

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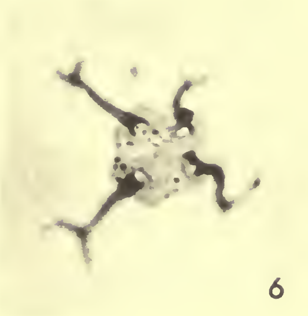

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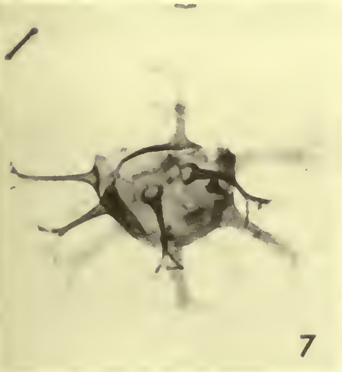

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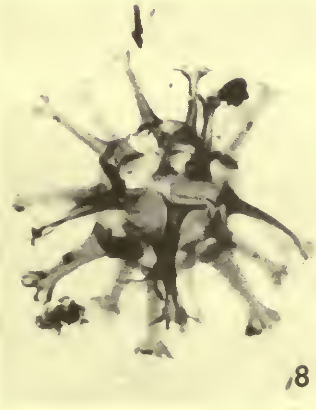

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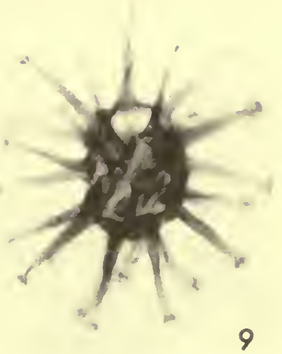

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PLATE 6

Oligosphaeridium reniforme (Tasch)

FIG. 1. Lower Colorado, Saskatchewan (depth, 1023 feet). Slide Sas 1023/1. × 500.

Tanyosphaeridium variecalamum Davey & Williams

FIG 2 Holotype. Slide PF 3035 (2) × 500

FIG 5 Lower Chalk, Compton Bay (28 feet above base of Chalk). Precingular, cingular and postcingular processes aligned into three series. Slide CB 5/C × 500

Litosphaeridium siphoniphorum (Cookson & Eisenack)

Lower Chalk, Fetcham Mill Borehole.

FIG. 3. Lateral view showing precingular and postcingular processes, and antapical process. Slide PF. 3987 (depth, 730 feet). × 500.

FIG. 4. Detached operculum. Slide FM 690/14 (depth, 690 feet). × 975.

Callaiosphaeridium asymmetricum (Deflandre & Courteville).

FIG. 6. Upper Greensand, Fetcham Mill Borehole (depth, 886 feet). Lateral view illustrating epitractal archaeopyle. Slide FM 886/2. × 500.

Cleistosphaeridium polypes (Cookson & Eisenack)

FIG. 7. Upper Woodbine Formation. Enlargement to show process extremities. Slide T5/3. × 975.

FIG. 8. Lower Chalk, Compton Bay (151 feet above base of Chalk). Specimen possessing apical archaeopyle. Slide CB 21/C. × 500.

Cleistosphaeridium polypes var. ***clavulum*** nov.

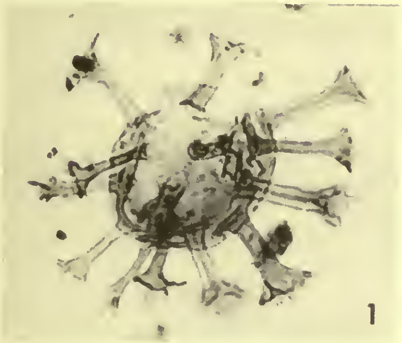
FIG. 9. Type. Slide PF. 3995 (1) × 500.

FIG. 10. Lower Chalk, Fetcham Mill Borehole (depth, 840 feet). Enlargement to show process extremities. Slide PF. 3035. × 975.

?Cleistosphaeridium aciculare sp. nov.

FIG. 11. Upper Colorado, Saskatchewan (depth, 835 feet). Specimen with numerous fine processes. V. 51988. × 500 (phase contrast).

FIG. 12. Holotype. V. 51979 (3). × 500.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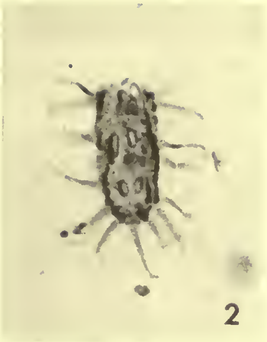
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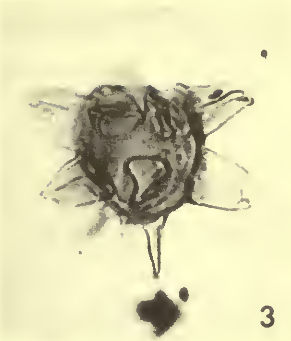
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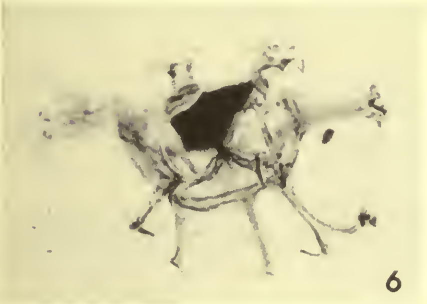
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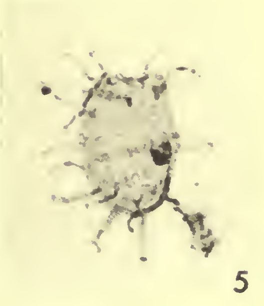
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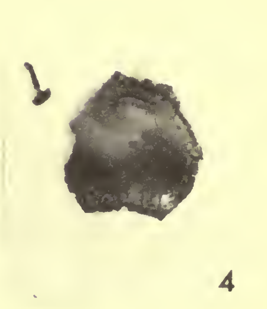
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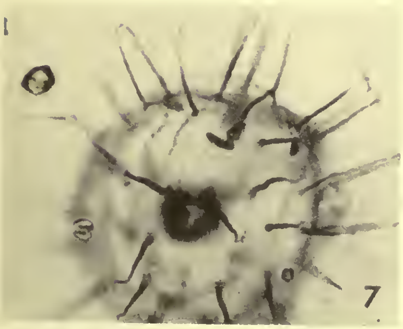
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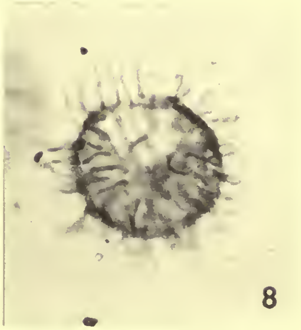
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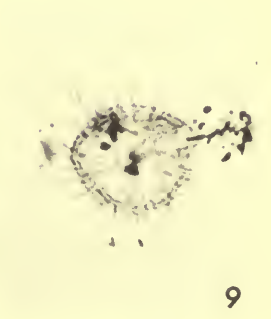
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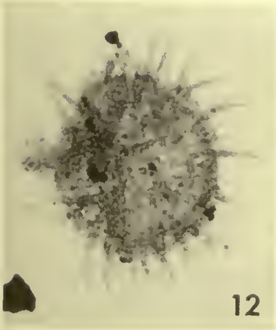
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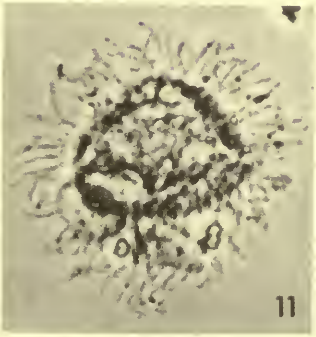
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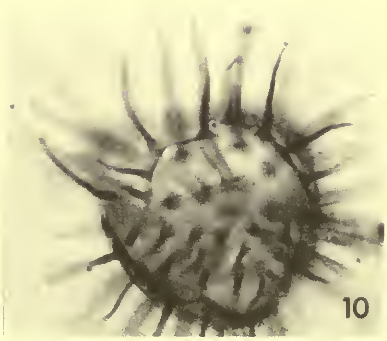
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PLATE 7

Exochosphaeridium striolatum var. **truncatum** nov.

FIG. 1. Lower Chalk, Fetcham Mill Borehole (depth, 750 feet). Apical view showing two partially detached precingular plates to the north. Slide PF. 3988. × 500.

FIG. 2. Type; precingular archaeopyle clearly shown to be formed by the removal of two plates. V. 51982 (1). × 500.

FIG. 3. Lower Chalk, Escalles Borehole (depth, 165 metres). Detached operculum composed of two precingular plates. V. 51981. × 500.

?Cleistospaeridium flexuosum Davey *et al.*

FIG. 4. Lower Chalk, Fetcham Mill Borehole (depth, 690 feet). Slide PF. 3030. × 500 (phase contrast).

Exochosphaeridium phragmites Davey *et al.*

FIG. 5. Lower Chalk, Escalles Borehole (depth, 165 metres). Apical process with precingular archaeopyle to the north-west. V. 51981. × 500.

Cleistosphaeridium huguonioti var. **pertusum** nov.

FIG. 6. Lower Chalk, Fetcham Mill Borehole (depth, 690 feet). Enlargement showing vacuolated processes with small distal bifurcations. Slide FM 690/14. × 975.

FIG. 7. Type. Slide PF. 3040 (2). × 500.

FIG. 9. Lower Chalk, Escalles Borehole (depth, 159 metres). Specimen possessing apical archaeopyle. Slide E 159/4. × 500.

Cleistosphaeridium heteracanthum (Deflandre & Cookson)

FIG. 8. Lower Chalk, Compton Bay (137 feet above base of Chalk). Slide CB 19/2. × 500.

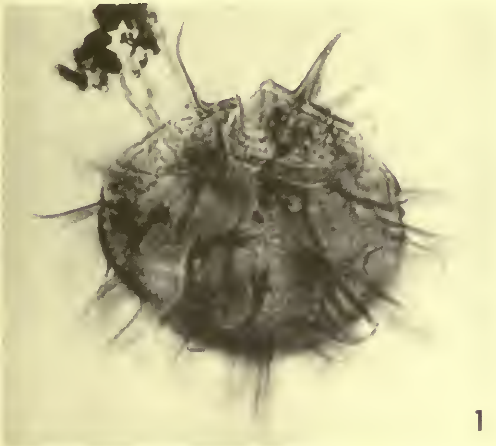
Cleistosphaeridium huguonioti (Valensi)

FIG. 10. Lower Chalk, Fetcham Mill Borehole (depth, 730 feet). Detached operculum. Slide FM 730/19. × 975.

?Cleistosphaeridium parvum sp. nov.

FIG. 11. Holotype. V. 51981 (3). × 975.

FIG. 12. Lower Chalk, Escalles Borehole (depth, 159 metres). Cingular region devoid of processes clearly visible. Slide E 159/1. × 975.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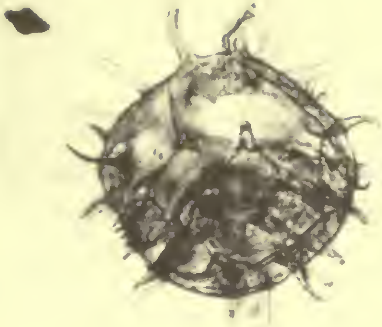
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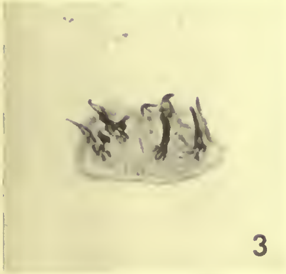
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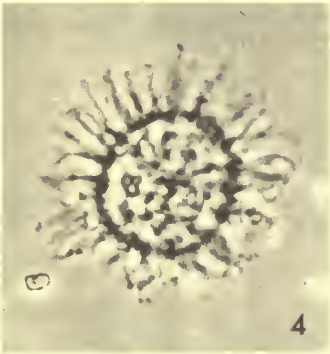
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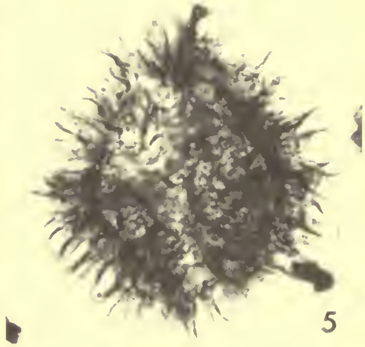
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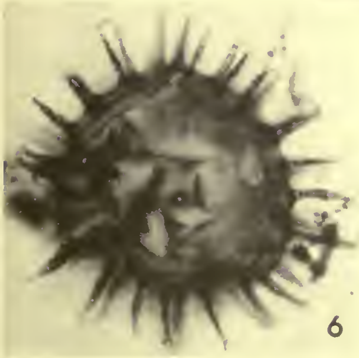
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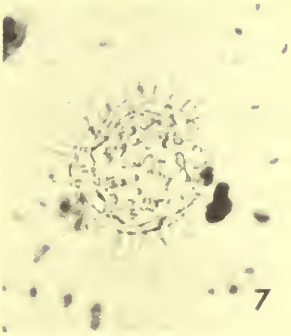
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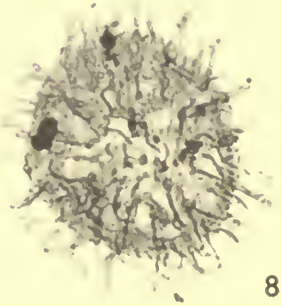
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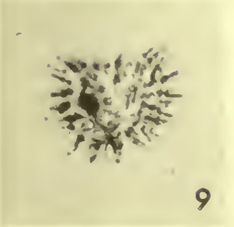
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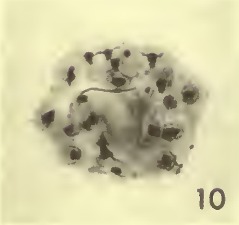
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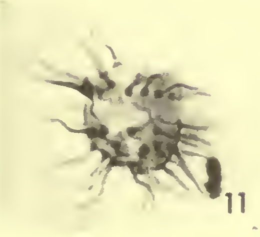
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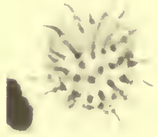
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PLATE 8

Cleistosphaeridium armatum (Deflandre)

FIG. 1. Lower Chalk, Escalles Borehole (depth, 189 metres). View of apical archaeopyle. Slide E 189/4. × 975.

FIG. 2. Lower Chalk, Compton Bay (116 feet above base of Chalk). Enlargement to show process extremities. Slide CB 17/C. × 975.

FIG. 12. Lower Chalk, Compton Bay (116 feet above base of Chalk). Slide CB 17/C. × 500.

Cyclonephelium eisenacki sp. nov.

FIG. 3. Lower Colorado, Saskatchewan (depth, 1,023 feet). Specimen with archaeopyle developed. V.51980. × 500.

FIG. 4. Holotype. V. 51980 (2). × 500.

Prolixosphaeridium conulum sp. nov.

FIG. 5. Holotype; complete specimen. V. 51981 (5). × 500.

FIG. 6. Lower Chalk, Compton Bay (59 feet above base of Chalk). Apical archaeopyle to the north. Slide CB 9/2. × 500.

Cleistosphaeridium multifurcatum (Deflandre)

FIG. 7. Lower Chalk, Escalles Borehole (depth, 207 metres). View of apical archaeopyle. Slide E 207/5. × 500.

FIG. 10. Lower Chalk, Compton Bay (15 feet above base of Chalk). Complete specimen. V. 51986. × 500.

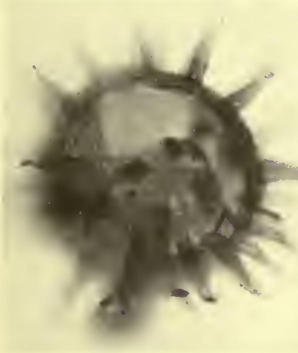
Coronifera oceanica Cookson & Eisenack

FIG. 8. Lower Chalk, Fetcham Mill Borehole (depth, 730 feet). Specimen possessing an apical archaeopyle and an antapical process. Slide FM 730/13. × 500.

FIG. 11. Lower Chalk, Escalles Borehole (depth, 189 metres). Complete specimen. Slide E 189/4. × 500.

Surculosphaeridium longifurcatum (Firtion)

FIG. 9. Lower Chalk, Fetcham Mill Borehole (depth, 730 feet). Lateral view to show apical archaeopyle, deeply furcate precingular processes and completely subdivided cingular processes. Slide PF. 3987. × 500.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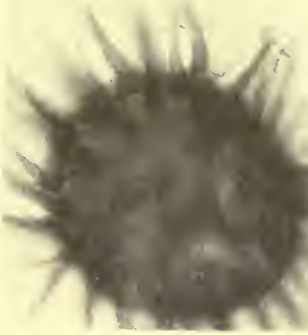
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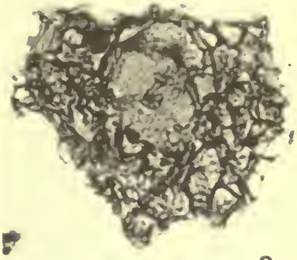
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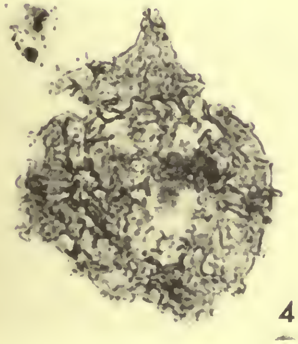
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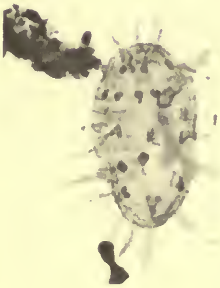
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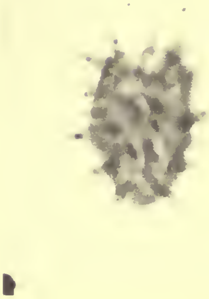
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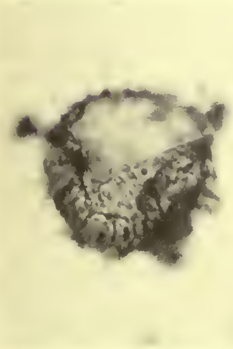
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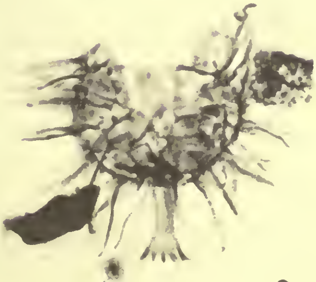
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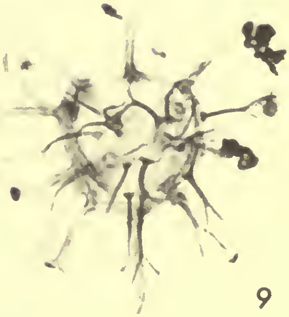
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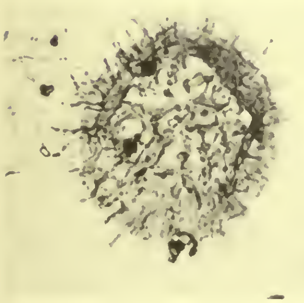
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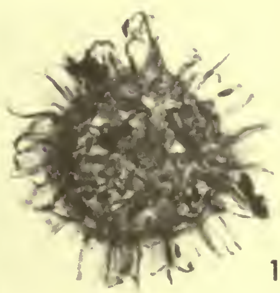
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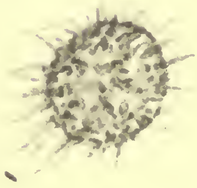
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PLATE 9

Cyclonephelium paucispinum sp. nov.

FIG. 1. Holotype. V. 51981 (2). × 500.

FIG. 2. Lower Chalk, Compton Bay (15 feet above base of Chalk). Complete specimen with operculum partially detached. V. 51986. × 500.

Cyclonephelium vannophorum sp. nov.

FIG. 3. Enlargement of holotype to show apical archaeopyle, and the shape of the processes. V. 51986 (1). × 975.

Cyclonephelium eisenacki sp. nov.

FIG. 4. Lower Colorado, Saskatchewan (depth, 1,023 feet). Complete specimen. Slide Sas 1023/3. × 500.

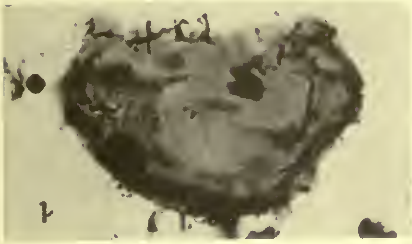
Hystrichokolpoma ferox (Deflandre)

Lower Chalk, Fetcham Mill Borehole (depth, 840 feet). Slide FM 840/11.

FIG. 5. Lateral view (bottom of specimen by transparency) showing precingular, cingular and postcingular processes; large antapical process to the south and fine sulcal processes to the west. × 500.

FIG. 6. Medial section. × 500.

FIG. 7. Lateral view (top of specimen) showing precingular, cingular and postcingular processes. × 500.



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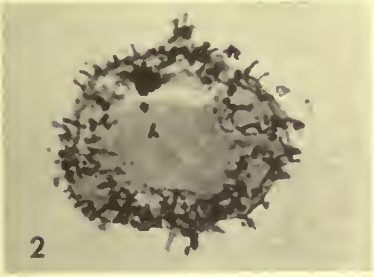

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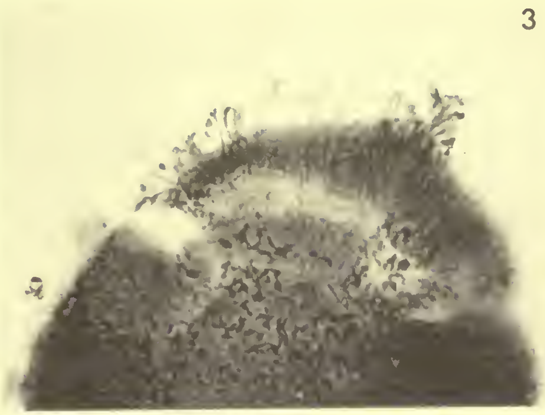

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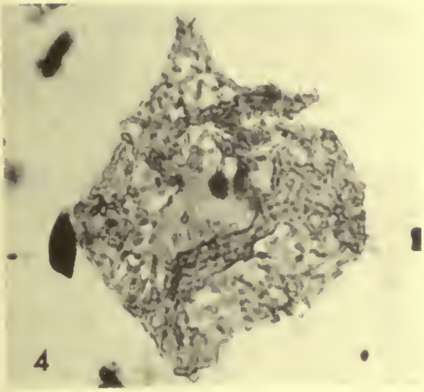

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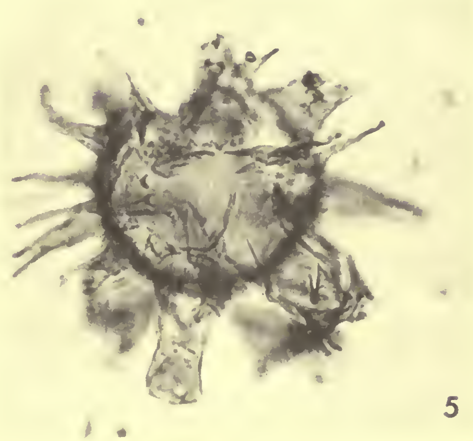

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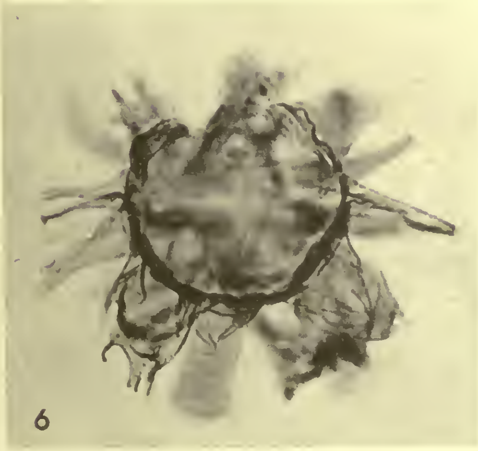

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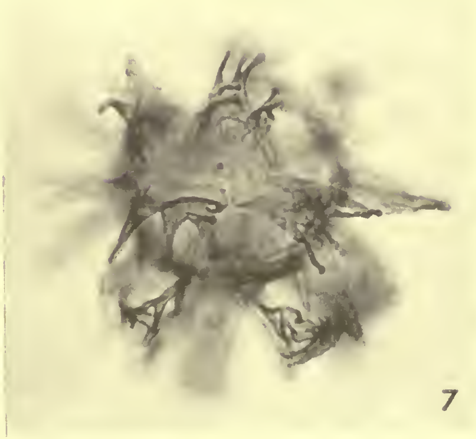

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PLATE 10

Hystrichosphaera ramosa var. ***ramosa*** (Ehr.)

Lower Chalk, Fetcham Mill Borehole (depth, 750 feet).

FIG. 1. Ventral surface. Slide PF. 3988. × 500.
FIG. 2. Dorsal surface with precingular archaeopyle. Slide PF. 3988. × 500.
FIG. 5. Detached operculum (boring depth, 770 feet). Slide FM 770/15. × 500.

Hystrichosphaera ramosa var. ***multibrevis*** Davey & Williams

Lower Chalk, Fetcham Mill Borehole.

FIG. 3. Slide PF. 3988 (depth, 750 feet). × 500.
FIG. 4. Slide PF. 3988 (depth, 750 feet). × 500.

Hystrichodinium voigti (Alberti)

Lower Chalk, Escalles Borehole.

FIG. 6. Archaeopyle to the north-east. V. 51982 (depth, 159 metres).

FIG. 10. Detached operculum bearing 4 processes. Slide E 165/1 (depth, 165 metres). × 500.

Achomosphaera ramulifera (Deflandre)

FIG. 7. Lower Chalk, Escalles Borehole (depth, 159 metres). Specimen showing precingular archaeophyle and apical process. V. 51982. × 500.

Hystrichodinium dasys sp. nov.

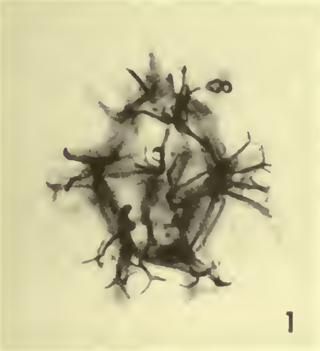
FIG. 8. Holotype illustrating cingulum. V. 51982 (3). × 500.

FIG. 9. Middle Chalk, Fetcham Mill Borehole (depth, 520 feet). Specimen with unusually stout processes proximally. Slide FM 520/7. × 500.

Adnatosphaeridium chonetum (Cookson & Eisenack)

FIG. 11. Lower Chalk, Escalles Borehole (depth, 165 metres). Complete specimen, V. 51981. × 500.

FIG. 12. Lower Chalk, Fetcham Mill Borehole (depth, 730 feet). Apical archaeopyle present. Slide PF. 3987. × 500.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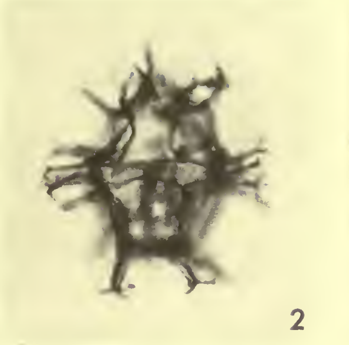
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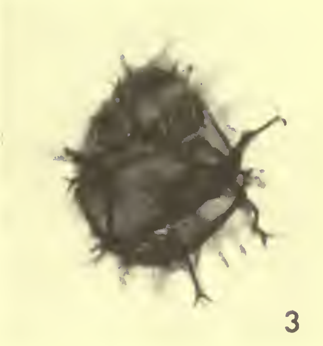
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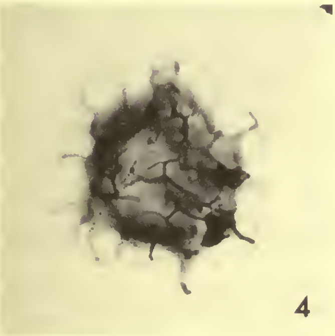
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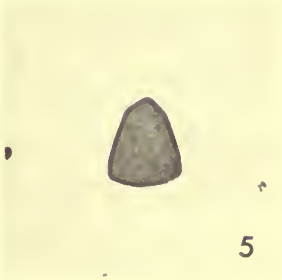
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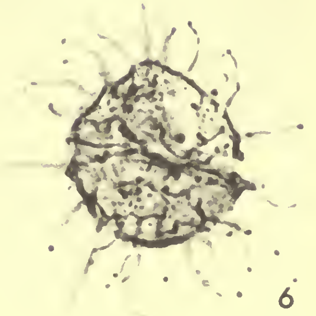
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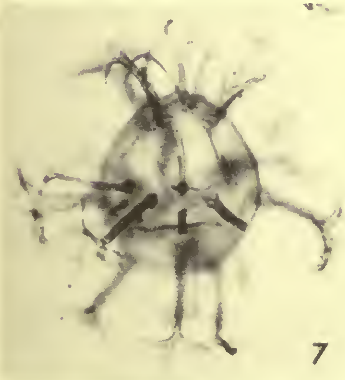
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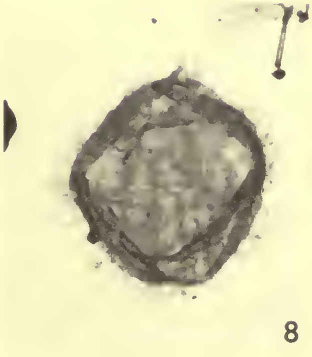
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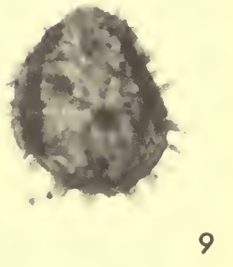
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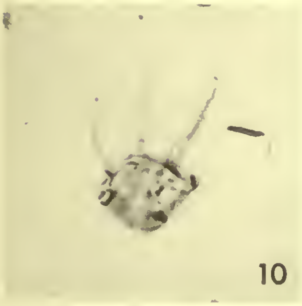
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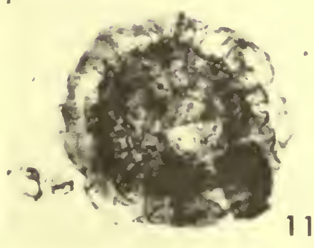
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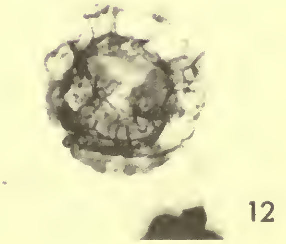
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PLATE 11

Trichodinium castaneum (Deflandre).

Lower Chalk, Escalles Borehole.

FIG. 1. Lateral view showing precingular archaeopyle and cingulum, V. 51989 (depth, 195 metres). × 500.

FIG. 2. Dorsal view showing small apical horn. Slide E 159/2 (depth, 159 metres). × 500.

FIG. 3. Complete specimen possessing a cingulum and possibly a sulcus, Slide E 189/4 (depth, 189 metres). × 500.

Exochosphaeridium pseudohystrichodinium (Deflandre)

Lower Chalk, Escalles Borehole.

FIG. 4. Complete specimen with operculum partially detached, V. 51982 (depth, 159 metres). × 500.

FIG. 5. Complete specimen illustrating pitted surface, V. 51981 (depth, 165 metres). × 500.

Cyclonephelium distinctum Deflandre & Cookson

FIG. 6. Lower Chalk, Escalles Borehole (depth, 159 metres). Specimen with unusually long processes, V. 51982. × 500.

FIG. 7. Lower Chalk, Escalles Borehole (depth, 159 metres). Complete specimen; archaeopyle in the act of developing. V. 51989. × 500.

FIG. 8. Lower Chalk, Compton Bay (15 feet above base of Chalk). Typical specimen with archaeopyle developed. V. 51986. × 500.

FIG. 10. Lower Chalk, Escalles Borehole (depth, 165 metres). Detached operculum. V. 51981. × 500.

Cyclonephelium membraniphorum Cookson & Eisenack

FIG. 9. Lower Chalk, Escalles Borehole (depth, 153 metres). Apical archaeopyle well illustrated. Slide E 153/3. × 500.

Cyclonephelium vannophorum sp. nov.

FIG. 11. Holotype with operculum partially detached. V. 51986 (1). × 500.

FIG. 12. Lower Chalk, Compton Bay (15 feet above base of Chalk). Specimen with apical archaeopyle developed. V. 51986. × 500.

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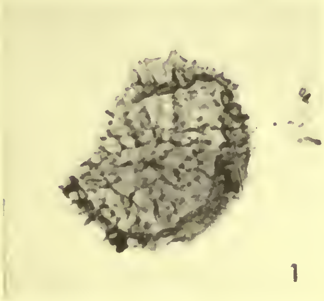
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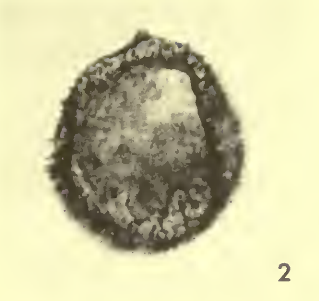
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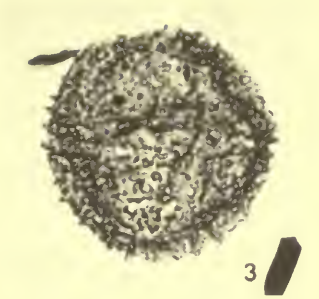
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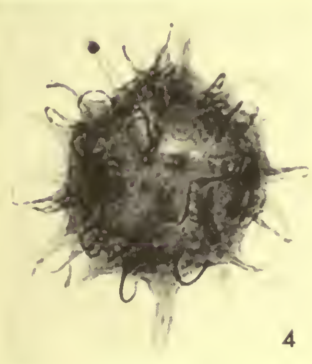
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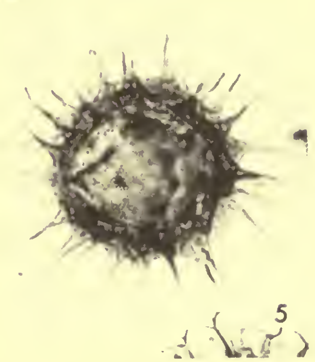
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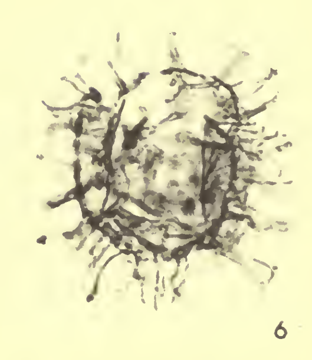
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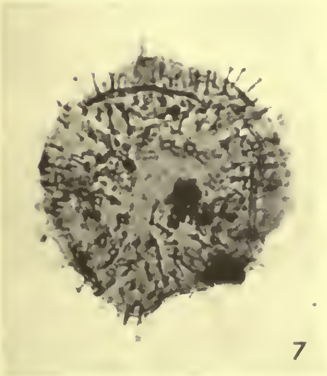
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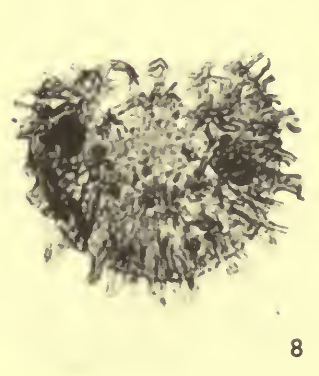
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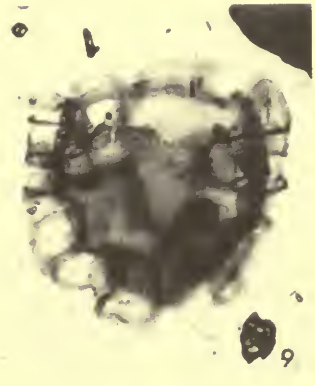
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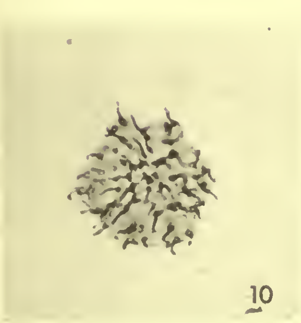
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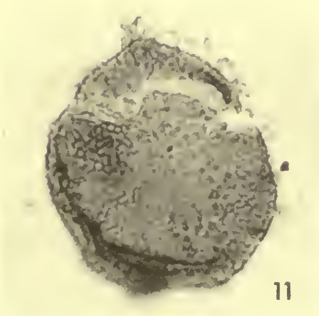
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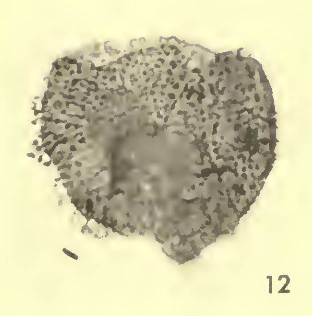
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PRINTED IN GREAT BRITAIN
BY ADLARD & SON LIMITED
BARTHOLOMEW PRESS, DORKING

A REDESCRIPTION OF W. CARRUTHERS' TYPE GRAPTOLITES

ISLES STRACHAN

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
GEOLOGY Vol. 17 No. 4
LONDON: 1969

A REDESCRIPTION OF W. CARRUTHERS' TYPE GRAPTOLITES

BRITISH MUSE
17 JAN 196
NATURAL HISTOR

BY

ISLES STRACHAN

Pp. 181–206; 5 *Plates*; 8 *Text-figures*

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THE BULLETIN OF THE BRITISH MUSEUM (NATURAL HISTORY), *instituted in* 1949, *is issued in five series corresponding to the Departments of the Museum, and an Historical series.*

Parts will appear at irregular intervals as they become ready. Volumes will contain about three or four hundred pages, and will not necessarily be completed within one calendar year.

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This paper is Vol. 17, *No.* 4 *of the Geological (Palaeontological) series. The abbreviated titles of periodicals cited followthose of the World List of Scientific Periodicals.*

World List abbreviation:
Bull. Br. Mus. nat. Hist. (Geol.).

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TRUSTEES OF
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Issued 17 *January*, 1969 *Price* £1 4*s*.

A REDESCRIPTION OF W. CARRUTHERS' TYPE GRAPTOLITES

By ISLES STRACHAN

CONTENTS

Page

I. INTRODUCTION 183
II. DESCRIPTIONS 185
Leptograptus capillaris 185
Pleurograptus linearis 186
Dicellograptus elegans 187
Dicellograptus moffatensis 189
Dicranograptus clingani 190
Climacograptus minimus 191
Climacograptus minutus 193
Cryptograptus tricornis 194
Monograptus clingani 195
Monograptus intermedius 196
Diversograptus? capillaris 198
Rastrites maximus 200
Cyrtograptus murchisoni 202
" *Dendrograptus* " *lentus* 204
III. REFERENCES 204

SYNOPSIS

The fourteen species of graptolites described and figured by William Carruthers, mainly in his paper of 1868, are redescribed from the type material where possible. Two neotypes are proposed. Some of the species appear to be unsatisfactory by modern standards, but it is hoped that refiguring of the types will assist future work.

I. INTRODUCTION

IN their monograph of British Graptolites (1901–18) Elles & Wood described and figured most of the previously known species as well as numerous new forms. In many cases, however, they did not use the original type material either because it was not available or because later collections had provided other, sometimes better, material. In the fifty years which have elapsed since then, discrimination of graptolite species has become keener, particularly by workers overseas who have frequently, in their subdividing, formally designated type specimens without consideration of the availability or value of the early material. It seems appropriate that the species described in the nineteenth century should be re-examined so that these workers should be able to recognize the old species accurately with the aid of modern descriptions and illustrations. The work could be tackled systematically by genus and species but this involves consideration of generic and specific limits in deciding the scope of a paper. It is easier to treat the species for redescription by discussing one author at a time and I hope to undertake further papers of a similar scope to this.

William Carruthers (1830–1922) was born at Moffat, Dumfriesshire, and early developed an interest in the local geology, particularly in the graptolites for which the area had then recently become famous through the researches of Harkness and Salter. His own publications on graptolites are comparatively few in number but it is clear that by 1867 he was regarded as an expert on the group, since he contributed the article on graptolites to the fourth edition of Murchison's " Siluria ". In the following year he described more fully the new species erected in that memoir. He strongly disagreed with Nicholson on the interpretation of a number of graptolite features and they carried on an acrimonious correspondence in the pages of the Geological Magazine during 1867. At the same time he was also describing fossil plants, to which he later devoted all his research. In 1870–72 he was assisting the young amateur John Hopkinson with his descriptions of new species of graptolites from the Moffat Shales but they both appeared to realize that the publication in 1876 of Lapworth's paper on " Scottish Monograptidae " marked a new and more critical approach to graptolite systematics and stratigraphy and neither of them published further papers on the subject. It is, however, clear from Lapworth's later papers that he maintained a friendly association with Hopkinson and Carruthers and the latter's manuscript notes on graptolites are in the Lapworth Library, Birmingham University. These notes contain no indication of how or when Lapworth acquired them but there are no references to papers after 1872 and it is possible that Carruthers gave them to Lapworth before taking up more administrative duties at the British Museum (Natural History) in 1880 and confining his research to palaeobotany.

The new species described by Carruthers are found in two main papers, in 1858 and 1868. The first of these was reprinted the following year in a more accessible journal and, as already mentioned, the 1868 paper described properly the species which were only illustrated in the appendix to " Siluria ". Carruthers had some harsh remarks to make about Nicholson's drawings of graptolites and, on the whole, his own are generally sufficiently accurate to allow recognition of the type specimens. Most of these were catalogued at once in the British Museum (Natural History) collections where they can be traced. Almost all his species can be recognized fairly easily. The type of *Rastrites maximus* is the only one which has not been found and a neotype is proposed for that species.

It is a pleasure to acknowledge the ready co-operation which I have had from those at the British Museum (Natural History) who have had charge of the graptolite collections and to thank their photographers who have provided most of the illustrations for the plates. I must also express my thanks to the Geological Survey & Museum and to the Royal Scottish Museum for the loan of specimens over a period which has been much longer than I had at first intended.

Specimens with Q numbers are in the British Museum (Natural History); with GSM, in the Institute of Geological Sciences, London; with BU, in the Geology Department, University of Birmingham; and with SM, in the Sedgwick Museum, Cambridge.

II. DESCRIPTIONS

Leptograptus capillaris (Carruthers)

Pl. 1

1868 *Cladograpsus capillaris* Carruthers: 130, pl. 5, figs. 7, 7a.
1876 *Leptograptus capillaris*(Carr.) Lapworth : 9, pl. 3, fig. 72.
1903 *Leptograptus capillaris* (Carr.); Elles and Wood : 112, pl. XV, figs. 4a–d.
?1954 *Leptograptus capillaris* (Carr.); Sherrard : 95, pl. 11, fig. 8.

Original description. " Extremely slender polypary, with remote branches and very minute hydrothecae; about twenty-four in an inch. It is not so abundant as *C. linearis*, and is easily distinguished by its capillary appearance. It is probably the same species as that figured and described by Emmons in his American Geology, vol. i, p. 109, pl. 1, fig. 7, under the name of *Nemagrapsus capillaris*. Loc. Moffat ".

Comments on usage. There appears to have been little confusion over this species. Although he quoted Emmons' species, Carruthers clearly intended his own form to rank as a new species and the American form is now referred to *Thamnograptus*. The original description refers to " remote branches " which are not shown by the type specimens or original figure but one illustration of *Cladograpsus linearis* of the previous year (Carruthers 1867, pl. 2, fig. 17a) shows the characteristic curved stipes with secondary branches. The original of this has not however been recognized.

TYPE MATERIAL. The syntypes, British Museum (Natural History) Q.30, were refigured by Elles & Wood. As lectotype I select the large rhabdosome on the upper right of Carruthers' original figure (see Pl. 1, fig. 2). The precise locality and horizon are not known but Elles & Wood give it as Hartfell Spa?, Hartfell Shales.

DIAGNOSIS. Very slender *Leptograptus* with markedly curved stipes, maximum breadth 0·5 mm. thecae eight to ten per cm.

REVISED DESCRIPTION. The species normally occurs crowded on the slabs so that details of the stipes are not readily seen. The sicula is inconspicuous but the stipes appear to grow initially horizontally or even somewhat downward before curving gracefully upwards and inwards, forming loops on occasion. The stipes widen from an initial breadth of 0·2 mm. to a maximum of 0·5 mm. over a distance of at least 4 or 5 cm. and appear to be twisted so that the thecae can appear on either side of the curve. The sicula is 2 mm. long and about 0·2 mm. wide but details of the origin of the stipes are not known. The thecae appear to be simple leptograptid tubes but the preservation of the distal parts of the stipes is such as to make measurements of their length and overlap impossible.

GEOLOGICAL HORIZON. Lapworth (1878) recorded the species only from the zone of *Pleurograptus linearis* but Elles & Wood (1903) also recorded it from the zone of *Dicranograptus clingani*. The type slab shows no associates, nor do most of the specimens in the Lapworth Collection. Lithologically, however, the slabs agree with the upper part of the Lower Hartfell Shales.

DISTRIBUTION. This species is known from only a few localities in the South of Scotland and is not recorded from beds of a similar age in South Wales. Ruedemann and Decker recorded it from the Viola Limestone in Oklahoma but gave no figures (Ruedemann 1947). Sherrard (1954) recorded it from New South Wales but her figure shows stipes which appear to be too broad and not curved enough. They may be one of the forms of *Leptograptus flaccidus* which occurs about the same horizon, e.g. *L.f. arcuatus* Elles & Wood. Thomas (1960) illustrated a form which is clearly not *L. capillaris* as the stipes are too straight, and this then casts doubt on the range of the species as given by Thomas, which goes up to the Ashgill Series.

Pleurograptus linearis (Carruthers)

Pl. 2; Figs. 1a–c

1858 *Cladograpsus linearis* Carruthers : 467, fig. 1.
1859 *Cladograpsus linearis* Carruthers: 24, fig. 1.
non 1867 *Cladograpsus linearis* Carruthers; Carruthers : 369, pl. 2, fig. 17.
?1867a *Cladograpsus linearis* Carruthers; Carruthers : 540, fig. 8.
1867 *Pleurograpsus linearis* (Carruthers) Nicholson : 257, pl. 11, figs. 1–5.
1868 *Cladograpsus linearis* Carruthers; Carruthers : 129.
1876 *Pleurograptus linearis* (Carruthers); Lapworth, pl. 3, fig. 69.
1904 *Pleurograptus linearis* (Carruthers); Elles & Wood : 119, pl. 16, fig. 7, pl. 17, fig. 1.

Original description. "From a short and very slender base the zoophyte divides into two stems, each supporting the cells on their upper sides. Branches are given off at irregular intervals from these principal stems. The length of the polypidom is very great; one specimen I have been able to trace for nearly three feet . . . The polypidom at its origin, near to the slender base, is very narrow, being little more than a fine line; as it increases in length it increases in breadth, until it is fully two-fifths of a line broad. The cells are very remote from each other, and are, at first sight, from the slight indentation they make in the stem, scarcely perceptible, giving the Graptolite the appearance as if it were a clear line. The mouth of the cell is straight and at right angles to the axis; it makes an indentation equal to about one-sixth of the breadth of the polypidom. The number of cells in an inch is about eighteen. Type locality Hartfell."

Comments on usage. Carruthers' later figures (?1867, 1867a) are different from his original but there has been no difficulty in the recognition of his species. Carruthers accepted Nicholson's specimen of *Pleurograpsus linearis* although he was very critical of the detail of the figures. Nicholson's specimen was refigured by Elles & Wood who also figured a variety *simplex* in which the branches are much more widely spaced.

Type material. Carruthers' original specimen is in the British Museum (Natural History), Q.848, and the counterpart is amongst material presented to the Royal Scottish Museum, Edinburgh, by Carruthers in 1858 (RSM 1858.10.4). Nicholson's specimen, Q.27, was said by Elles & Wood to be the type specimen but it is clearly not. The lower of the two large specimens on the type slab has four lateral branches and is recognizable as the specimen figured in 1858 (see Pl. 2, figs. 1, 2).

Revised description. Rhabdosome consisting of two or three main stipes arising from the sicula with secondary branching on one or both sides. Stipes up to 1 mm. broad; thecae simple leptograptid, about eight per cm., with apertural excavations occupying about one-third of the rhabdosome breadth. The sicula is not seen on any of the figured material and is probably associated in older rhabdosomes with one of the branches, a feature also seen in species of *Leptograptus* where a third branch may be developed. Young specimens on the type slab, however, suggest that the sicula is about 2 mm. long. The stipes are initially very slender but show some secondary thickening in older specimens where the thecae on the main stipes are difficult to distinguish. There is considerable variation in the branching, Nicholson's specimen (Pl. 2, fig. 3) being much stiffer than Carruthers' or the other specimen figured by Elles & Wood in which the tertiary branched stipes are aligned in flowing curves. This suggests that the variation in attitude of the stipes is simply a depositional effect.

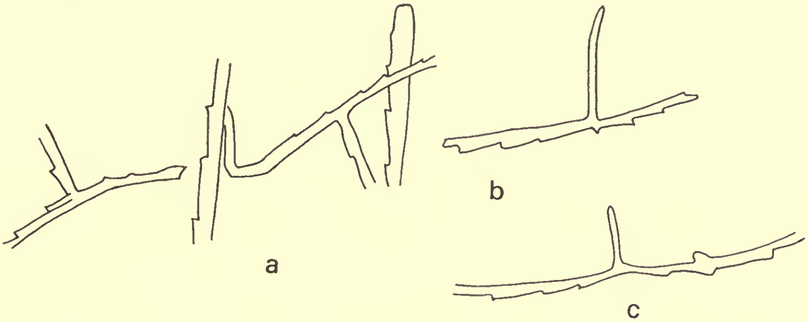

FIG. 1. *Pleurograptus linearis* Carr. a. Enlargement of proximal part of main stipe showing 2 lateral branches and possible central branch from the sicula. Counterpart of type slab, R.S.M. 1858.10.4. The 2 parallel distal parts of branches are the left hand pair from the holotype (Pl. 2, fig. 1). b, c. Young specimens showing sicula, type slab, Q.848. All ×5.

DISTRIBUTION. *P. linearis* appears to be confined to the one horizon in the south of Scotland where, however, it is quite common if all the fragments showing this type of branching really belong to it. Ruedemann (1908; 1947) figured a single specimen from the Utica Shale of New York State which shows similar branching at rather more distant intervals, approximating in that respect to var. *simplex* which is also recorded by Thomas (1960) from Australia.

Dicellograptus elegans (Carruthers)

Pl. 3, fig. 1.; Figs 2a, b.

1867 *Didymograpsus elegans* Carruthers : 369, pl. 2, fig. 16a.
1868 *Didymograpsus elegans* Carruthers; Carruthers : 129, pl. 5, figs. 8a, ?d.
1871 *Dicellograpsus elegans* (Carruthers) Hopkinson : 24, pl. 1, fig. 3.
1876 *Dicellograptus elegans* (Carruthers); Lapworth, pl. 4, fig. 87.
1877 *Dicellograptus elegans* (Carruthers); Lapworth : 141, pl. 7, fig. 8.
1904 *Dicellograptus elegans* (Carruthers); Elles & Wood : 159, pl. 23, figs. 2a–e.
?1947 *Dicellograptus elegans* (Carruthers); Ruedemann : 380, pl. 63, fig. 1.
1954 *Dicellograptus elegans* (Carruthers); Sherrard, pl. 10, fig. 6.

ORIGINAL DESCRIPTION. " Branches of the polypary divaricating at various angles, and with a slight curve within a short distance of the proximal origin of the polypary. The hydrothecae are rounded at the apex, and free throughout a considerable portion of their length and the intervening spaces are rounded at the base; about twenty-two cells in an inch. The initial process is obvious in young specimens, but I have not been able to detect it in old individuals; the outer apex of the angle ornamented with three short strong spines. Loc. Moffat ".

COMMENTS ON USAGE. Since Elles & Wood refigured the type specimen there has been no difficulty with this species. The originals of Carruthers' figures 8b and 8c (BM(NH) Q.54) were recognized by Hopkinson (1871) as being a distinct species (*D. morrisii* Hopkinson) and not merely young stages of *elegans* as Carruthers thought.

TYPE MATERIAL. The holotype, Q.850 (Pl. 3, fig. 1), is from the Hartfell Shales, Dobbs Linn. The species appears to be commonest in the *P. linearis* Zone but the associates on the type slab (*Dicellograptus pumilus* and *Climacograptus* spp.) give no direct confirmation of horizon.

DIAGNOSIS. *Dicellograptus* with markedly introverted thecae and with distinct sigmoid curvature of stipes near proximal end, so that the stipes curve first upwards, then outwards, then upwards again.

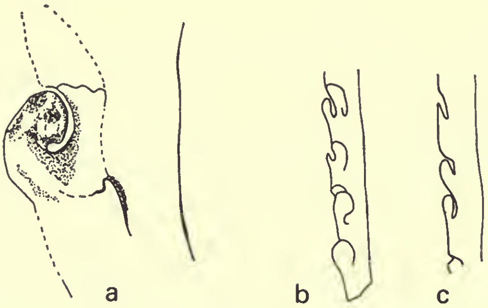

FIG. 2. *Dicellograptus* spp. a. *D. elegans* Carr. Detail of thecal aperture in proximal part of stipe. Q.850. ×30. b. *D. elegans* Carr. Distal thecae. Q.850. ×5. c. *D. moffatensis* Carr. Distal thecae. Q.843. ×5.

REVISED DESCRIPTION. The proximal double curvature is quite distinctive and the stipes have an almost uniform width of 1 mm. throughout their length. The first two thecae have prominent apertural spines which, with the virgella, give the three-spined proximal end noted by Carruthers. The thecae number eight to ten per cm. and are of the strongly introverted type with marked ventral curvature (group IV of Elles & Wood, which however are not introtorted, see Bulman 1944 : 37).

GEOLOGICAL HORIZON. Lapworth (1878) and Elles & Wood (1904) recorded the species only from the *P. linearis* zone, but in the summary range chart at the end of the Monograph, Elles & Wood also recorded it as common in the underlying zone of *D. clingani*. Elles (1925) also recorded it from both zones so its precise range must await a revision of the Hartfell Shales. Foreign records are surprisingly scanty but it seems to occur in Australia at the same horizon.

Dicellograptus moffatensis (Carruthers)

Pl. 3, figs. 5, 6; Fig. 2c

1858 *Didymograpsus Moffatensis* Carruthers : 469, fig. 3.
1859 *Didymograpsus Moffatensis* Carruthers; Carruthers : 26, fig. 3.
1868 *Didymograpsus Moffatensis* Carruthers; Carruthers : 129.
1871 *Dicellograpsus Moffatensis* (Carruthers) Hopkinson : 25, pl. 1, fig. 4.
1875 *Dicellograptus moffatensis* (Carruthers); Hopkinson & Lapworth : 654, pl. 34, fig. 5a.
1877 *Dicellograptus Moffatensis* (Carruthers); Lapworth : 141, pl. 7, fig. 9.
1904 *Dicellograptus moffatensis* (Carruthers); Elles & Wood : 157, pl. 23, figs. 1a–f.

ORIGINAL DESCRIPTION. " The base terminates in three distinct spinous processes. The zoophyte bifurcates from the base. The general appearance is like the figure; or occasionally the lines form an acute angle for about a quarter of an inch, then suddenly expand in slight curves, almost at right angles, for a short distance, when they again recur to their original direction. The branches are united for about a quarter of a line by a slight web, which in some specimens is terminated in a fine process of short length, taking the direction of a line bisecting the angle. The cells are arranged in the outer margins; they are very remote, and penetrate the polypidom to scarcely one-fourth of its breadth; they form slight openings on the margin of the polypidom, first entering at a right angle, and then suddenly turning downwards. These openings are lengthened ovate pouches, answering exactly in shape and size to the cell-serratures of the margin. The number of cells in an inch is about twenty. The breadth of the polypidom is about two-thirds of a line. Type locality Hartfell ."

COMMENTS ON USAGE. In 1868, Carruthers noted *D. divaricatus* (Hall) and *D. anceps* (Nicholson) as synonyms of his own species but this is merely a reflection of the confused state of graptolite systematics at the time. Elles & Wood refigured Carruthers' type but the species does not seem to have been widely recognized.

TYPE MATERIAL. This is one of the few species of which Elles & Wood made any discussion of type specimens. They considered that Carruthers' specimen was not a satisfactory type and that a specimen from the Lapworth Collection should be taken as the type. Carruthers' original figure is admittedly poor (Pl. 3, fig. 5) but the type slab shows three specimens which agree fairly well with it and show the essential characters of the species. The abrupt widening of the stipes on Lapworth's specimen, which Elles & Wood wanted as a character of the species, appears to be the result of slight shearing.

It is impossible to decide which of the three specimens was the original of Carruthers' figure so the specimen (Q.843) figured by Elles & Wood is here selected as lectotype (see Pl. 3, fig. 6). It is from the Hartfell Shales of Hartfell and is associated on the slab with *Orthograptus* cf. *whitfieldi*. This probably indicates a low horizon in the Hartfell Shales. Lapworth (1878) records it no higher than the zone of *Climacograptus wilsoni*.

REVISED DESCRIPTION. Stipes sub-parallel initially, then diverging making an angle of about 45°, sometimes later converging. Stipes widening from an initial breadth of 0·4 mm. to a maximum of about 1·5 mm. Thecae eight to ten per cm., with markedly curved ventral walls and introverted apertures. The proximal end usually shows a membrane in the axil of the stipes, obscuring the sicula. The virgella and first thecal spines variably developed. The thecae are poorly preserved but distally appear to be very similar to those of *D. elegans* (Fig. 2c).

It is unfortunate that both Carruthers and Hopkinson included *D. divaricatus* (Hall) in their synonymy of this species as it makes it difficult to establish what they regarded as the diagnostic features of the species. The general shape of the rhabdosome appears to be the most characteristic feature, particularly the narrow axil and later divergence. In this respect the specimen figured by Elles & Wood in their Monograph (pl. 23, fig. 1c) is not at all typical but its only associates are the pair of specimens figured on the same plate (pl. 23 fig. 1b) which have the typical shape. As the rhabdosomes were flexible in life to some extent, this poses the problem of how much reliance should be placed on rhabdosome shape as a specific character in *Dicellograptus* and other forms with long slender stipes. *D. moffatensis* can be readily separated from other British *Dicellograptus* by size and shape of rhabdosome, *D. morrisii* Hopkinson being the most similar but with a more open axil. *D. moffatensis* var. *alabamensis* Ruedemann 1908 is not related at all and is clearly a *Dicranograptus*, close to *D. brevicaulis* Elles & Wood 1904.

Distribution. Elles & Wood recorded the species widely throughout the British Isles but it seems doubtful now if it occurs in the Lake District. The specimen figured by Hopkinson & Lapworth from Llanvirn (SM.A17400) is a poorly-preserved, bent dichograptid (O. M. B. Bulman, personal communication). The specimen from Abereiddy Bay refigured by Elles & Wood may well come from the locality referred to the "Dicranograptus Shales" (Cox, 1915 : 304) and not from the *D. murchisoni* Shales for which the area is best known. If this is so, the species ranges from ?Llandeilo Series to Caradoc Series (*wilsoni* Zone). It has been recorded from Australia but Thomas (1960) does not list it in his range chart and so presumably does not consider it to be present. Linnarsson recorded it from Scania but Hadding (1913) transferred this form to his new species *D. vagus*.

Dicranograptus clingani Carruthers

Pl. 3, figs. 2–4; Fig. 3a

1868 *Dicranograptus Clingani* Carruthers : 132, pl. 5, figs. 6a–c.
1870 *Dicranograptus Clingani* Carruthers; Hopkinson : 358, pl. 16, figs. 4a–c.
1876 *Dicranograptus Clingani* Carruthers; Lapworth, pl. 3, fig. 76.
1877 *Dicranograptus Clingani* Carruthers; Lapworth : 141, pl. 6, fig. 43.
1904 *Dicranograptus Clingani* Carruthers; Elles & Wood : 165, pl. 24, figs. 1a–i.
1915 *Dicranograptus Clingani* Carruthers; Hadding : 22, pl. 3, figs. 1–8.

Original description. "Polypary with a short diprionidian portion, the proximal end furnished with three very delicate spines; hydrothecae forming a slight serration along the margin; twenty-one cells in the inch. Loc. Moffat."

Comments on usage. Elles & Wood put this species in a group by itself on the basis of the thecal characters—approximately straight ventral walls and horizontal apertures. These characters are clearly seen in Hopkinson's figures and serve to differentiate the species from other forms with a short biserial portion.

TYPE MATERIAL. Elles & Wood refigured as " type specimen " the original of Carruthers' fig. 6a and this can be taken as a designation of a lectotype. The specimen, Q.55 (Pl. 3, figs. 3, 4), is from the Hartfell Shales, Hartfell Spa. Carruthers' fig. 6b, Q.842 (Pl. 3, fig. 2), is also from this locality.

REVISED DESCRIPTION. *Dicranograptus* with short biserial portion consisting of three or four pairs of thecae, and short, straight uniserial stipes diverging at about 40°. The biserial portion has a uniform breadth of about 1 mm. and the branches are similarly uniform at about 0·8 mm. The virgella is usually prominent as a short spine and the first two thecae may have sub-apertural spines. The ventral walls of the later thecae are straight and the apertures are horizontal in excavations which occupy about one-third of the breadth. The uniserial stipes appear to be rarely more than 2 cm. long although Hadding figures a specimen with stipes nearly 4 cm. long. The distal thecae number eight to ten per cm. but the stipes are usually twisted so that the thecae are in scalariform view (Fig. 3a) and it is difficult to decide the precise thecal shape. The apertural excavations are clearly marked by lists and it is probable that the straight ventral walls of the proximal thecae continue in the distal ones.

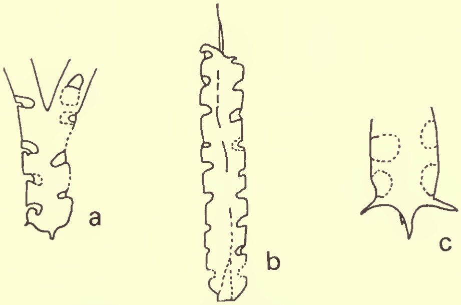

FIG. 3. a. *Dicranograptus clingani* Carr. Proximal end of paratype. Q.842. ×5. The right hand side of the specimen is poorly preserved. b. *Climacograptus minutus* Carr. Lectotype. Q80. ×5. c. *Cryptograptus tricornis* Carr. Proximal end of lectotype showing basal spines. Q1299. ×5.

DISTRIBUTION. The species is common in the Lower Hartfell Shales of the Moffat area and is also found at Conway. Elles & Wood recorded it from equivalent beds in Ireland. It is found in Scandinavia but has not been recorded from North America. Thomas (1960) gives records but omits it from his range chart, so casting doubt on the records. The type specimen has no associates but Elles & Wood recorded it only from its own zonal association.

Climacograptus minimus (Carruthers)

Pl. 4, fig. 3; Fig. 4c

1868 *Diplograpsus minimus* Carruthers : 74, 130, pl. 5, figs. 12a, b.
?1906 *Climacograptus minimus* (Carruthers) Elles & Wood : 191, pl. 27, figs. 1a–g.

ORIGINAL DESCRIPTION. " This agrees with *D. pristis* in general appearance, and in the form and arrangement of the cells, except that the whole polypary and all its parts are so very small. Had I met with only a few specimens, I would have considered it as merely an accidental variety, but I have seen so many, all agreeing in size, that I cannot doubt that it is a good species, especially as young specimens of *D. pristis* early attain their full breadth, and the increase of the polypary is by addition to its distal end, and not to the size of the already formed hydrothecae, just as in the living *Sertulariadae*. About thirty-eight cells to one inch. Loc. Moffat."

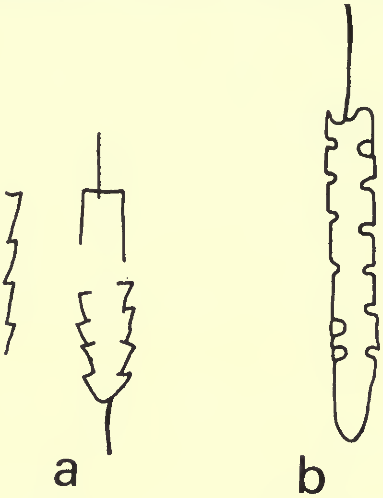

FIG. 4. Figures to show Carruthers' clear distinction between his two small species of diplograptid. a, Copy of original MS drawing of " *Diplograptus minimus* " which has appended note " 38 to inch ". b, Similar copy of *Climacograptus minutus* which has notes " 32 to 40 to an inch, nearly opposite ".

COMMENTS ON USAGE. In his 1868 paper, Carruthers clearly distinguished two small biserial species and Fig. 4, taken from his notebook, illustrates his ideas of the differences, one clearly climacograptid, the other what he called diplograptid (now orthograptid). His type slab however shows a large number of small, poorly-preserved rhabdosomes which appear to be almost all climacograptid and Elles & Wood certainly regarded his species in this light. In his description of the species (1868 : 130) he called it *Diplograpsus minutus* although elsewhere, in the explanation of the plate published in the first part of the paper (1868 : 74), he called it *D. minimus*, agreeing with his MS notes, and usage of this prior name avoids the homonym which results from the transference of the species to *Climacograptus*.

Elles & Wood did not re-figure Carruthers' material, and their specimens, from the Hartfell Shales (*clingani* and *linearis* Zones), reach a breadth of 2 mm. Carruthers' specimens on the type slab are only about 1 mm. wide and are associated with some slender uniserial stipes, which look very like *Monograptus* sp. (*atavus* or *acinaces* type). It thus seems probable that Elles & Wood's species is not the same as Carruthers' but it is clear from the foreign references (e.g. Ross & Berry 1963, Obyt & Sobolevskaya 1964) that it is Elles & Wood's species which is nowadays recognized under this name. Carruthers' original notes are of little use since the only measurements he gives are the thecal numbers per inch. A sketch of " *Diplogr. minimus* " clearly shows thecae of an orthograptid type in accordance with his comparison of it with *D. pristis* but, as mentioned above, the common form on the type slab appears to have climacograptid thecae. The species must remain for the moment in an unsatisfactory state since a proper appraisal of Elles & Wood's form must await critical re-examination of the Upper Ordovician climacograptids.

TYPE MATERIAL. Q.82, a slab crowded with poorly-preserved specimens.

REVISED DESCRIPTION. The rhabdosome is about 1 mm. wide and up to 10 mm. long. Thecal details are obscure.

HORIZON. As noted above, the type slab shows slender uniserial stipes very similar to monograptids of the *vesiculosus* and *cyphus* Zones, in contrast with the description by Elles & Wood of the species from the Hartfell Shales (*clingani* and *linearis* Zones).

Climacograptus minutus Carruthers

Pl. 4, fig. 1, ; Figs 3b, 4b

1868 *Climacograptus minutus* Carruthers : 132, pl. 5, fig. 10a.
?1906 *Climacograptus minutus* Carruthers; Elles & Wood : 211, pl. 27, figs. 12a–c.

ORIGINAL DESCRIPTION. " This is a very minute but well-marked species, never attaining a greater size then represented on the Plate. There are at the rate of from thirty-two to forty cells in the space of an inch. Loc. Moffat."

COMMENTS ON USAGE. This species does not seem to have been widely recorded, probably because of its unsatisfactory nature. Carruthers' original specimens are of widely differing widths and Elles & Wood based their account of the species on other material from the British Museum (Natural History). Packham (1962) revised some of the British Silurian diplograptids but did not discuss this species. His *C. tangshanensis linearis* appears to be close to Carruthers' fig. 10b (1868).

TYPE MATERIAL. Carruthers' original specimens can be recognized and appear to be of two different forms. His fig. 10a (Q.80) is here selected as lectotype (Pl. 4, fig. 1). The original of fig. 10b (Q.1372) is a narrower form and fits well with *Climacograptus scalaris miserabilis* Elles & Wood. Elles & Wood's figured material (Q.849) is all somewhat distorted and it is clear that they did not use Carruthers' original specimens for their description, probably through some confusion with " *Diplograptus minutus* ".

REVISED DESCRIPTION. Rhabdosome 7 mm. long. 1·2 mm. broad; thecae thirteen per cm., with large excavations occupying about one quarter of the breadth of the rhabdosome and about equal to the length of the free ventral wall. The apertures are nearly opposite each other (as recorded in Carruthers' notes) and not alternate as stated by Elles & Wood. The proximal end of the type specimen is poorly preserved but there appears to be a stout virgula which is prolonged beyond the distal end of the rhabdosome. The type specimen is completely flattened and it is not possible to make out any details of a median septum.

The uniform breadth of the rhabdosome and the large opposite excavations combine to make this form quite distinct from other British climacograptids. Unfortunately the range of variation is not known and since the type specimen has no associates, its precise horizon is also doubtful. It remains therefore an unsatisfactory species.

Cryptograptus tricornis (Carruthers)

Pl. 4, figs. 4–6; Fig. 3c

1858 *Diplograpsus tricornis* Carruthers : 468, fig. 2.
1859 *Diplograpsus tricornis* Carruthers; Carruthers : 25, fig. 2.
1867 *Diplograpsus tricornis* Carruthers; Carruthers : 290, pl. 1, figs. 10a–d.
1868 *Diplograpsus tricornis* Carruthers; Carruthers : 131, pl. 5, fig. 11a, b.
1880 *Cryptograptus tricornis* (Carruthers) Lapworth : 171, pl. 5, figs. 27a–e.
1908 *Cryptograptus tricornis* (Carruthers); Elles & Wood : 296, pl. 32, figs. 12a–d.
1908 *Cryptograptus tricornis* (Carruthers); Ruedemann : 443, pl. 28, figs. 1–4.
1913 *Cryptograptus tricornis* (Carruthers); Hadding : 40, pl. 2, figs. 13–14.
1915 *Cryptograptus tricornis* (Carruthers); Hadding : 325, pl. 6, fig. 15.
1934 *Cryptograptus tricornis* (Carruthers); Hsu : 87, pl. 6, figs. 13a–m.
1937 *Cryptograptus tricornis* (Carruthers); Bulman : 5, t-fig. 8.
1945 *Cryptograptus tricornis* (Carruthers); Bulman : 29, pl. 2, figs. 1–8.
1960 *Cryptograptus tricornis* (Carruthers); Thomas, pl. 6, fig. 69.

ORIGINAL DESCRIPTION. " This species can be readily distinguished by the three spines which adorn its base, and which are almost always preserved. The central spine is a continuation of the line of the axis; it is shorter than the lateral ones . . . The polypidom is more slender than in *D. foliaceus*, which in general outline it somewhat resembles. The axis is slender, and produced beyond the other parts of the fossil. The cell-walls are well marked, extending upwards from the axis to the boundary of the fossil. Each cell forms a rhomb whose outer border is slightly indented, giving the boundary of the fossil a faintly serrated aspect. When the fossil is preserved so as to show the serratures, the spines are so compressed that the central one is almost or altogether lost. When the spines are well preserved and in the position described, no traces of the individual cells are discernible; the boundary of the fossil is an unbroken line ".

In 1868, Carruthers added " When I described this species I had not detected the mouths of the cells in those specimens in which they should have been shown on the upper surface. In more perfectly preserved specimens since obtained these have been beautifully shown ".

COMMENTS ON USAGE. This species has been widely recognized as it is easily identified from the original description and figures. Lapworth (1880) discussed the varying appearance of the thecae at some length and introduced the genus *Cryptograptus* for this and allied species. Hadding (1915) showed by comparison with *Glossograptus* that the two stipes were in lateral contact (the monopleural arrangement of Jaanusson 1960) and removed the genus from the Diplograptidae. The structure of the proximal end was not, however, elucidated until 1938 when Bulman described isolated specimens from the Balclatchie Limestone and the two different aspects of the basal spines noted by Carruthers was explained. A number of varieties have been described, differing mainly in the breadth of the rhabdosome.

DIAGNOSIS. Rhabdosome biserial, monopleural, 2–4 cm. long widest at base when preserved in lateral view, maximum width 1·8 mm. but typically narrower. Thecae ten to twelve per cm. Basal spines conspicuous, but short.

TYPE MATERIAL. BM(NH) Q.1299, presented to the museum in 1860, is almost certainly Carruthers' original slab. It is crowded with specimens up to 35 mm. long and 1·6 mm. broad but it is not possible to recognize the original figured specimens. Accordingly, one of the better specimens has been selected as lectotype (Pl. 4, fig. 4). The association on the slab includes abundant *Corynoides calicularis* Nich. Similar pieces in the Lapworth Collection (Birmingham University) are labelled " The Cornice, Hartfell " and, although this is not marked on Lapworths' published map of Hartfell, it would appear from the text that the horizon is lowest Hartfell, zone of *Climacograptus wilsoni*.

DESCRIPTION. No detailed description is needed since that in the Monograph is satisfactory and has been recently supplemented by Bulman's detailed account of isolated specimens. There seems to be some variation in the thecal count, specimens from Girvan having consistently higher (twelve to sixteen per cm.) counts. Elles & Wood described the variety *schaeferi* which Lapworth had figured earlier and claimed that it was " somewhat wider than the typical form ". Examination of the material in Lapworth's collection does not confirm this difference but there seems to be a difference in thecal shape and the basal spines are not conspicuous.

DISTRIBUTION. This species has been recorded from all continents and some of the more recent records are given in the synonymy. The stratigraphic range was given by Elles & Wood as Arenig Series (*extensus* Zone) to Caradoc Series (*clingani* Zone), a longer range than any other Ordovician species, and it is possible that critical examination of a large number of specimens from the lower horizons might show them to be distinct from the typical form from the early Caradoc. Sherrard (1954) records it from the zone of *P. linearis* but no illustration is given to confirm this.

Monograptus clingani (Carruthers)

Pl. 5, figs. 1–5

1867 *Graptolithus Clingani* Carruthers : 369, pl. 2, fig. 8.
1868 *Graptolithus Clingani* Carruthers; Carruthers : 127, pl. 5, figs. 19a, b.
1876 *Monograptus Clingani* (Carruthers); Lapworth, pl. 1, fig. 24.
1876*a* *Monograptus Clingani* (Carruthers); Lapworth : 501, pl. 20, figs. 3a–c.
non 1897 *Monograptus Clingani* (Carruthers); Perner, pl. 11, figs. 15–17.
1913 *Monograptus Clingani* (Carruthers); Elles & Wood : 463, pl. 46, figs. 11a–f.
1951 *Monograptus clingani* (Carruthers); Bulman : 322, t–fig. 5.
1956 *Monograptus clingani* (Carruthers); Bondarenko & Keller : 91, t-fig. 2.

ORIGINAL DESCRIPTIONS. 1867. ". . . a beautiful small species, which at first I referred to *G. millepeda*, M'Coy, but that species is certainly the proximal end of *G. Becki*, and this differs from it in having a very broad common base, from which the hydrothecae rise ." 1868. " Polypary, small and arcuate, with a broad common canal, and slender somewhat recurved hydrothecae. This beautiful little graptolite I long supposed to be only the proximal portion of some other species, but the large number I have met with, all equally perfect, none larger than fig. 19a, and many showing the prolongation of the axis beyond the distal end, together with the great breadth of the common canal (forming two-thirds of the breadth of the whole polypary), unlike the early portion or proximal fragment of any graptolite with which I am acquainted, have induced me to consider it a good species . . ."

COMMENTS ON USAGE. Carruthers' descriptions gave no real details of the species. From the syntypes it appears that two different species may be confused but as both are young rhabdosomes it is not possible to be sure. The characters of the proximal thecae are not determinable from the lectotype, chosen by Přibyl (1948), which is completely flattened but they appear to be of the *priodon* type with well marked hooks to the apertures (Pl. 5, fig. 5). The distal thecae are similar. Lapworth recorded a " Clingani Band ", some 6 inches thick, in his Dobbs Linn sections and numerous specimens in his collection bear this label. In a recent resurvey of the section, Toghill (1965) recognized the unit again but recorded *M. clingani* from a wider horizon.

TYPE MATERIAL. The specimen (Q.87) figured by Carruthers as fig. 19a was referred to as " type specimen " by Elles & Wood in the explanation of their plate and the second specimen called " co-type " (Q.84), leaving them perhaps of equal status. Přibyl (1948) however clearly stated that Carruthers' fig. 19a is the lectotype which is unfortunate as this specimen has a broader common canal than in most of the other specimens referred to the species. This may be only a preservational feature as specimens in the Lapworth collection from Duffkinnel, the type locality, are all of the common type in which the hooks occupy at least half of the breadth of the rhabdosome.

REVISED DESCRIPTION. Rhabdosome dorsally curved at the proximal end, distally becoming more or less straight; widening from an initial breadth of 0·6 mm. to a maximum of about 1·5 mm. within the first 6 or 7 mm. The thecae are of *priodon* type with about one-third of the length involved in the hook which occupies half of the breadth of the stipe. The shape of the thecae varies a good deal with the type of preservation but there appears to be no overlap of the thecae (Bulman 1951, fig. 5), the broad prothecal portion occupying the whole of the breadth of the rhabdosome.

DISTRIBUTION. Lapworth recorded the species in abundance from a 6-inch band within the *sedgwickii* Zone at Dobbs Linn, and Marr & Nicholson (1888) similarly had a *M. clingani* Band above their *convolutus* Zone in the Lake District. Elles & Wood apparently extended the *convolutus* Zone to include these horizons and also recorded the species from the *gregarius* Zone below in their summary table.

Monograptus intermedius (Carruthers)

Pl. 5, fig. 6; Fig. 5

1868 *Graptolithus intermedius* Carruthers : 126, pl. 5, fig. 18.
?1876a *Monograptus intermedius* (Carruthers) Lapworth : 316, pl. 10, figs. 10a, d.

non 1913 *Monograptus intermedius* (Carruthers); Elles & Wood : 485, pl. 49, figs. 3a–c.
?1952 *Spirograptus intermedius* (Carruthers); Münch, pl. 37b, figs. 7a, b.

ORIGINAL DESCRIPTION. " Polypary slender; proximal end composed of a slender canal with distant, isolated, and very small hydrothecae; adult hydrothecae, short, triangular, the upper margin of the cell forming an acute angle with the common canal. About twenty-six cells to an inch. This species differs from *G. Nilssoni*, *G. tenuis* and *G. Hisingeri* in the form of the cells, and from the last also in the slender common canal. Perhaps Portlock's figure 6a. pl. 19 of his Report belongs to this species. Loc. Moffat. "

COMMENTS ON USAGE. It is clear from the specimens in Lapworth's collection that he included under this name a number of slender forms which do not agree with Carruthers' type specimen. Elles & Wood used only one slab from the Lapworth Collection for their redescription of this species and the crowded fragments on it show thecae which are much more slender than those of the type specimen in which the thecae are nearer those of *M. involutus*. Lapworth considered that *M. acutus* (Hopkinson 1872) was the same as *M. intermedius* but Hopkinson quite clearly differentiated them. Most later workers have, however, apparently relied on Elles & Wood's account.

TYPE MATERIAL. Holotype, BM(NH) Q.88, Birkhill Shales, Moffat.

REVISED DESCRIPTION. Rhabdosome arcuate, with very slender proximal end, widening from about 0·3 mm. to a maximum of about 1·0 mm. in the distal part. Thecae of the *spiralis* type, the proximal ones with a slender prothecal portion and an abruptly widened apertural region, distal ones more uniformly widening, about ten thecae per cm. The proximal end of the type specimen is poorly preserved but appears to be comparatively straight so that the rhabdosome is not truly spirally curved in the way shown by *M. communis*, etc. On thecal shape, however, Münch's assignation of the species to *Spirograptus* is quite possible. In general shape and the slender proximal end, the species is close to *Spirograptus planus* (Barrande) as figured by Přibyl (1946, pl. 8, figs. 6–8) but that species rapidly reaches a breadth

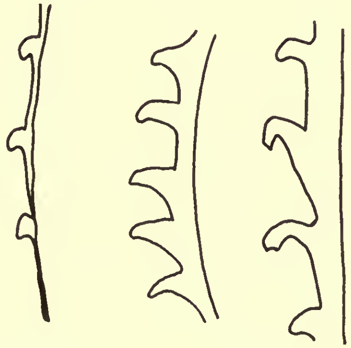

Fig. 5. Sketches of proximal, medial and distal thecae of *Monograptus intermedius*, holotype, Q.88, × 10 approx.

of more than 1·5 mm. and the rhabdosome continues to spiral distally. The species is here retained in *Monograptus* sensu lato.

DISTRIBUTION. The type specimen is associated with a proximal end of *M. triangulatus*-type and seems to be from the zone of *M. gregarius.* Most of the records appear to be based on Elles & Wood's description and hence are misidentified so that no distribution can be given at present.

Diversograptus? capillaris (Carruthers)

Fig. 6a, b.

1867 *Rastrites capillaris* Carruthers : 368, pl. 2, fig. 10.
1868 *Rastrites capillaris* Carruthers; Carruthers : 126, pl. 5, fig. 16.
non 1876a *Rastrites capillaris* Carruthers; Lapworth : 314, pl. 10, fig. 4.
1876a *Monograptus attenuatus* Hopkinson; Lapworth : 317, pl. 10, fig. 9.
?1897 *Monograptus* (*Rastrites*) *gemmatus* (Barrande); Perner, t-fig. 26.
1913 *Monograptus gemmatus* (Barrande); Elles & Wood : 436, pl. 43, figs. 5a–d, ?e.
1952 *Monograptus* (?subgenus) *capillaris* (Carruthers); Bouček & Přibyl : 206, t-fig. 4d–f.
1953 *Diversograptus capillaris capillaris* (Carruthers) Bouček & Přibyl : 496, 558, pl. 1, figs. 1–3.

ORIGINAL DESCRIPTION. " Common tube very slender, with short isolated triangular hydrothecae, their base of attachment to the common canal as long or longer than their depth. About sixteen cells to an inch. Loc. Moffat. Richter figures this specimen in *Zeitschr. Deutsch. Geol. Gesellsch.*,V, 1853, Tab. xii, fig. 34a, referring it to *R. gemmatus* Barr., which is very different, and of which his fig. 34b is a good representation ".

There has been considerable confusion over this slender species. Carruthers' original description is not clear and Hopkinson (1872) described *M. attenuatus* as another slender species without making detailed comparison with *capillaris.* Lapworth took the generic assignment to *Rastrites* as correct in spite of Carruthers' statement that the base of the triangular theca was longer than its height. From his own larger and more detailed collections from Dobbs Linn, Lapworth (1876a) redescribed *M. attenuatus* and a " *R. capillaris* " which is a true rastritid (see Fig. 6d). Perner (1897) redescribed *M. gemmatus* (Barrande) which has distinctly hooked thecae (Fig. 6c) but while he gave only a natural size figure of the holotype he also gave an enlarged drawing under the same name of a form with simpler thecae. It was apparently this enlarged figure which Elles & Wood took as typical of *M. gemmatus* and accordingly included *M. capillaris* Carr. and *M. attenuatus* Hopkinson in its synonymy. They do not seem to have considered Lapworth's drawings or specimens of " *R. capillaris* " (which are clearly distinct from Carruthers' types) although they refigured his specimens of *M. attenuatus.* Bouček & Přibyl (1952) re-examined the slender monograptids and showed clearly that Carruthers' and Hopkinson's species were distinct from *M. gemmatus.* In the following year they assigned diversograptid forms to *D. capillaris* and the species has been widely recorded as such in Central European work since 1952. Unfortunately British material has so far provided very few examples of diversograptid rhabdosomes while the German material (e.g. Manck 1924) is usually poorly preserved as far as thecal characters are concerned. It is thus doubtful if the equivalence of the British and Continental specimens can be regarded as proven.

Type material. Holotype Q.86, from the Birkhill Shales, Moffat.

Revised description. Rhabdosome only known as fragments, up to 5 cm. long, very slender, maximum breadth 0·4 mm.; thecae elongate triangular, about seven per cm., widening gradually from the initial prothecal portion, probably with no overlap. Apertures of *spiralis*-type but no spines seen.

Discussion. The type material is very poorly preserved and other slender British specimens are comparatively rare in collections, generally only found as small fragments. It is difficult to match these satisfactorily with the German and Bohemian material which, although more frequently showing complete rhabdosomes, is usually quite flattened and does not show thecal characters well. The slender

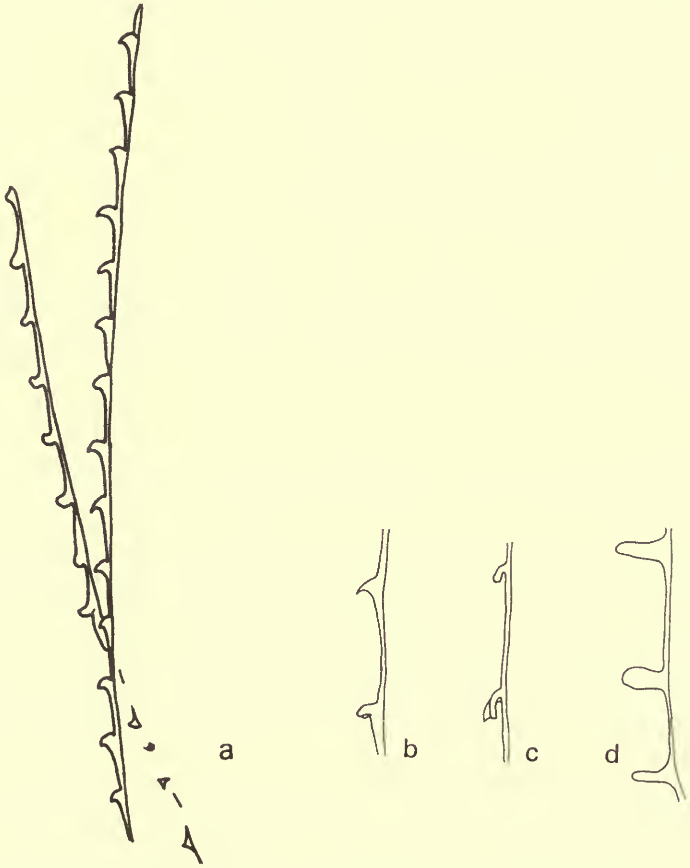

Fig. 6. *Diversograptus? capillaris* Carr. a. Copy from original drawing for Elles & Wood, pl. 43, fig. 5d. Holotype, Q.86. ×5. b. *D? capillaris* Carr. Two thecae for comparison with *M. gemmatus*. Q86. ×10. c. *M. gemmatus* Barr. Fragment of stipe with 2 thecae showing hooked apertures. *R. maximus* Beds, Belcraig Burn, Moffat. BU 304. ×10. d. *Rastrites* "*capillaris*" Lapw. (? = *R. spina* Richter) Duffkinnell. BU 305. ×10.

stipes appear to have been fairly flexible and the shape of the thecae is variable along the stipe, depending probably on the twisting of the stipe. Although it is quite clear that *D.? capillaris* is distinct from *M. gemmatus* (Barrande), its relationship to *M. attenuatus* Hopkinson remains doubtful. The specimens which Lapworth figured as *M. attenuatus* are obviously close to Carruthers' *capillaris* but these may be different from Hopkinson's types which have not yet been traced.

DISTRIBUTION. The type material is associated with *Rastrites* cf. *peregrinus*, indicating a Middle to upper Birkhill age which agrees with the records from the rest of Europe.

Rastrites maximus Carruthers

Pl. 5, fig. 7; Fig. 7a

1867a *Rastrites maximus* Carruthers : 540, fig. 90(6)
1868 *Rastrites maximus* Carruthers : 126, pl. 5, fig. 14.
1876a *Rastrites maximus* Carruthers; Lapworth, pl. 1, fig. 1.
1907 *Rastrites maximus* Carruthers; Törnquist : 15, pl. 2, figs. 28, 29, ?27, ?30–33, ?pl. 3, fig. 1.
1914 *Rastrites maximus* Carruthers; Elles & Wood : 494, pl. 50, figs. 6a–d, ?6e.
1941 *Rastrites maximus* Carruthers; Přibyl : 15.
?1955 *Rastrites maximus* Carruthers; Malinowska : 57, pl. 11, fig. 4.
1967 *Rastrites maximus* Carruthers; Schauer : 184, pl. 6, fig. 1.

ORIGINAL DESCRIPTION. " Common tube slender, supporting very large hydrothecae at wide intervals. Hydrothecae nearly half an inch long, somewhat enlarged towards the apex, and furnished at the base with a triangular corneus membrane extending a short distance up the margin of the cells. About six cells in an inch. Loc. Moffat. "

COMMENTS ON USAGE. This species has been recorded from a few places in Europe but appears to be replaced by *R. linnaei* Barrande in Central Europe. The large rastritids are usually found in a very fragmentary state owing to the extremely slender common canal, and isolated thecae cannot always be identified specifically since the thecal length/interspace ratio appears to be one of the most useful characters for discrimination. All the large forms, however, appear to occur about the same horizon and so are useful for stratigraphic purposes.

Although the species has been widely known and figured by Törnquist (1907) and other authors, no proximal ends appear to have been conclusively demonstrated. Most of the so-called " young specimens " have short, well-spaced thecae which may be broken or represent other species such as *R. distans*. Both Törnquist and Elles & Wood gave measurements for the first few thecae and the interspaces between them but examination of a large number of specimens from the Moffat area and from the Crossfell Inlier, Northern England, shows clearly that the long thecae of the adult develop within the first centimetre much more rapidly than was generally thought. Unfortunately few specimens are found with more than a few proximal thecae and it is difficult to separate *R. maximus* from *R. linnaei* and *R. distans* prior to the four or five theca stage.

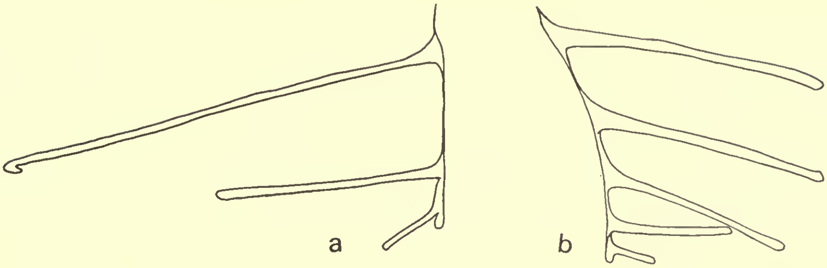

FIG. 7. Proximal ends of *Rastrites* spp. a, *R. maximus* Carr., neotype, BU 1692. b, *R. linnaei* Barr., BU 1700. Both × 5 aprox.

Table I gives the dimensions of some of these rhabdosomes but the data are as yet insufficient for a statistical analysis. The positions of theca 1 and th2 are the same in relation to the sicula in the three species, with th2 leaving the common canal at the apex of the sicula.

TABLE I

	length of theca				thecal interspace		
	1	2	3	4	1/2	2/3	3/4
R. maximus							
Törnquist 1907	1·0	2·7	6·2	1·7	1·0	1·4	1·7
Elles & Wood 1913	1·5	3·5	5·0	—	1·5	3·0	—
Neotype, BU 1692	1·4	5·3	10·2	12·0	0·8	3·0	4·5
Q.1390 BM(NH)	1·1	5·3	10·4	10+	0·8	1·6	4·0
R. linnaei							
BU 1700 (Elles & Wood, pl. 51, fig. 1b)	1·1	3·2	4·8	6·0	0·6	1·1	1·8
R. carnicus							
Seelmeier 1936	1·2	—	5·0	—		(0·1—0·3)	

TYPE MATERIAL. Carruthers' type specimen cannot be traced in the British Museum (Natural History) collections and although Q.1390 bears some resemblance to Carruthers' figure there are no details of locality or horizon for it. Accordingly a neotype is here proposed, chosen from the specimens figured by Elles & Wood. The specimen, B.U.1692 (Elles & Wood, pl. 50, fig. 6b) is from the Upper Birkhill Shales of Riskinhope Burn, Yarrow, Peeblesshire. (For stratigraphic details see Lapworth 1878 : 272).

REVISED DESCRIPTION. Adult thecae more than 10 mm. long (maximum observed 1·8 cm.) with interspaces about 5 mm; common canal very slender; base of theca characteristically enlarged with the proximal side at right angles to the common canal and the distal side somewhat oblique. Thecal apertures with a well-defined hook.

DISTRIBUTION. The species is known from many localities in the Moffat area and was recorded by Elles & Wood from the Lake District and North Wales.

Records from Sweden and Central Europe are doubtful although, as noted above, it is often impossible to determine specificially the fragmentary large rastritids. Amongst the Bohemian material in the Lapworth Collection there are no specimens approaching the typical form in length and spacing of the adult thecae. Recent records from Belgium (Legrand 1962) and Portugal (Romariz 1962) give no illustrations or dimensions and require confirmation. The specimen figured by Malinowska (1955) has a broad common canal although the thecae appear to be long enough. Schauer (1967) has figured a good specimen from Germany.

Cyrtograptus murchisoni Carruthers

Pl. 5, fig. 8, 9; Fig. 8

1867a *Cyrtograpsus Murchisonii* Carruthers : 540, foss. 90, fig. 1.
1868 *Cyrtograpsus Murchisonii* Carruthers; Carruthers : 128, pl. 5, figs. 17a, b.
?1899 *Cyrtograptus Murchisoni* Carruthers; Perner : 21, t-fig. 28.
1900 *Cyrtograptus Murchisoni* Carruthers; Elles, pl. 24, fig. 6.
1914 *Cyrtograptus Murchisoni* Carruthers; Elles & Wood : 505, pl. 51, figs. 3a–c.
?1933 *Cyrtograptus murchisoni* Carruthers; Bouček : 30, pl. 2, figs. 1–3.
non 1939 *Cyrtograptus murchisoni* Carruthers; Chang & Sun, pl. 1, figs. 4–8.

ORIGINAL DESCRIPTION. " Hydrothecae triangular apiculate, furnished with a spine. The upper margin of the cell at right angles to the axis, about twenty-eight cells to the inch. The polypary is considerably incurved at its proximal end, and as it grows it gradually opens into a larger curve. The branches spring from the celluliferous surface of the polypary, but as there is no break in the continuity of the hydrothecae, they must arise from the periderm covering the common canal. The branches also curve in the same direction as the main portion of the polypary. Loc. Pencerrig, Builth. I have associated the name of the author of ' Siluria ' with this remarkable species. The only British specimens I have seen are in the Geological Museum, Jermyn Street, but among the specimens obtained by the British Museum from M. Barrande there is a specimen from Listice, labelled *G. priodon*, which belongs to this species. "

COMMENTS ON USAGE. Carruthers' figure is somewhat idealized but there is no difficulty in recognizing the species. The syntypes are not well preserved and do not show the proximal end well on the large specimens although this may be the result of damage to the specimens which have at some stage been broken. This in unfortunate as Bouček, in his revision of the Cyrtograptidae (1933), distinguished forms with excentric proximal coiling from those with central (and more open) coiling. He had no forms of the first type with secondary branches (a characteristic of *murchisoni*) but he separated the simply-branched forms (*centrifugus* and *murchisoni bohemicus*) on the proximal ends. The type slabs of *murchisoni*, however, show proximal curvature of the *centrifugus* type and this was also figured by Elles & Wood.

It is reasonable to separate the simply-branched forms as a subspecies as there appears to be some stratigraphic value in this (see Rickards 1965) but if the curvature is also admitted as a diagnostic character, a new name is required for the Bohemian specimens of "*murchisoni*". If the proximal end is regarded as a variable feature within the species, then there is no good criterion for separating *centrifugus* from *m. bohemicus* and these may both be regarded as junior synonyms of Tullberg's *C. murchisoni* var. *crassiusculus*. Pending a revision with full stratigraphic details of these Lower Wenlock cyrtograptids, it seems best to restrict the present account to the redescription of Carruthers' syntypes and the numerous topotypes.

TYPE MATERIAL. Carruthers noted that his types were in the Jermyn Street Museum and the specimen and counterpart are now numbered GSM 10717–8. They are from the Wenlock Shale, Pencerraig, Builth, Radnorshire.

REVISED DESCRIPTION. Rhabdosome stout, proximal end forming a helical spiral with triangular thecae of the *spiralis* type. First-order cladia curved, arising at well-spaced intervals (about five to eight thecae between each) and bearing secondary branches which are generally curved in the same direction. Thecae on the distal part of the main stipe and on the cladia have a tubular proximal part and a short, hooked aperture. The change takes place on the main stipe after the third or fourth cladium. Thecae ten to fourteen per cm.

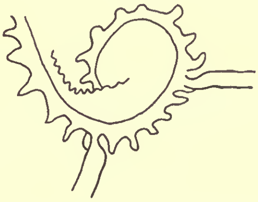

FIG. 8. *Cyrtograptus murchisoni* Carr. Poorly preserved proximal end showing excentric coiling. The most proximal thecae are underneath the later part of the main stipe. GSM 10717. ×3.

DISTRIBUTION. As noted above, there is some difficulty in matching Bouček's description of the Bohemian material with the British types, although Carruthers recognized the species in material from Listice. The stout, secondarily branched forms appear near the base of the Wenlock throughout Europe and it appears convenient to regard them all as one species. Further geographic variation may be noticed when well-preserved material from other areas is studied. The species has been recorded from Canada but so far without confirmatory illustrations. The form recorded from China appears to be the earlier species, *Monograptus spiralis*. Russian records (Obut 1964; Obut, Sobolevskaya & Bondarev 1965) appear to be of the species group but not the typical form. The relationship of *C. murchisoni* to the forms with only first order branches is still unknown but the latter seem slightly earlier stratigraphically (Rickards 1965) and could well be ancestral. The absence of cyrtograptids from the succeeding zone of *M. riccartonensis* suggests that the later *C. rigidus* and its allies are not phylogenetically related to *C. murchisoni*, since this would involve a reversal of the trend towards more numerous branches.

In my notes on British zones (Strachan 1960) I observed that *C. murchisoni* was "apparently unknown outside the type locality". Since then I have seen many-branched specimens from the Wenlock of the South of Scotland and Rickards (1965) has also found numerous specimens in the Lake District.

Dendrograptus lentus Carruthers

1867a *Dendrograptus lentus* Carruthers: 541, foss. 90, fig. 5.
1868 *Dendrograptus lentus* Carruthers: 130, pl. 5, fig. 5.

The specimen described under this name is preserved in the Geological Survey & Museum, GSM 10691 (and counterpart 10692). The species was noted by Wood (*in* Elles & Wood, p. lvii) as belonging to *Clonograptus* and a note on the specimens says " ?Shineton Shales, Shrops. " Carruthers recorded the species as " Caradoc, Co. Fermanagh " and the specimens are listed as such in the Survey Catalogue of 1878. However there is a collection number with the drawing of this species in Carruthers' notes and this appears in the Survey Catalogue of 1864 as " *Graptolithus* sp. Cambrian, Wrekin. " There thus is some confusion over this species and since the name has not been used, so far as I can ascertain, since the original descriptions it is best regarded as a *nomen dubium*, and an appropriate recommendation to the ICZN has been made. If the species were to be regarded as valid, the name *lentus* would have priority over the widely used name *tenellus*, and these fragments are too poor to be the basis of this well-known species.

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EXPLANATION OF PLATES

Most of the specimens are in the British Museum (Natural History) and their numbers bear the prefix Q. Those with prefixes GSM and BU are in the Institute of Geological Sciences and Birmingham University respectively.

PLATE 1

Leptograptus capillaris (Carruthers)

FIG. 1. Copy of original figure, Carruthers 1868, fig. 7a.
FIG. 2. Type slab, Q.30, natural size. Hartfell shales. Hartfell Spa.

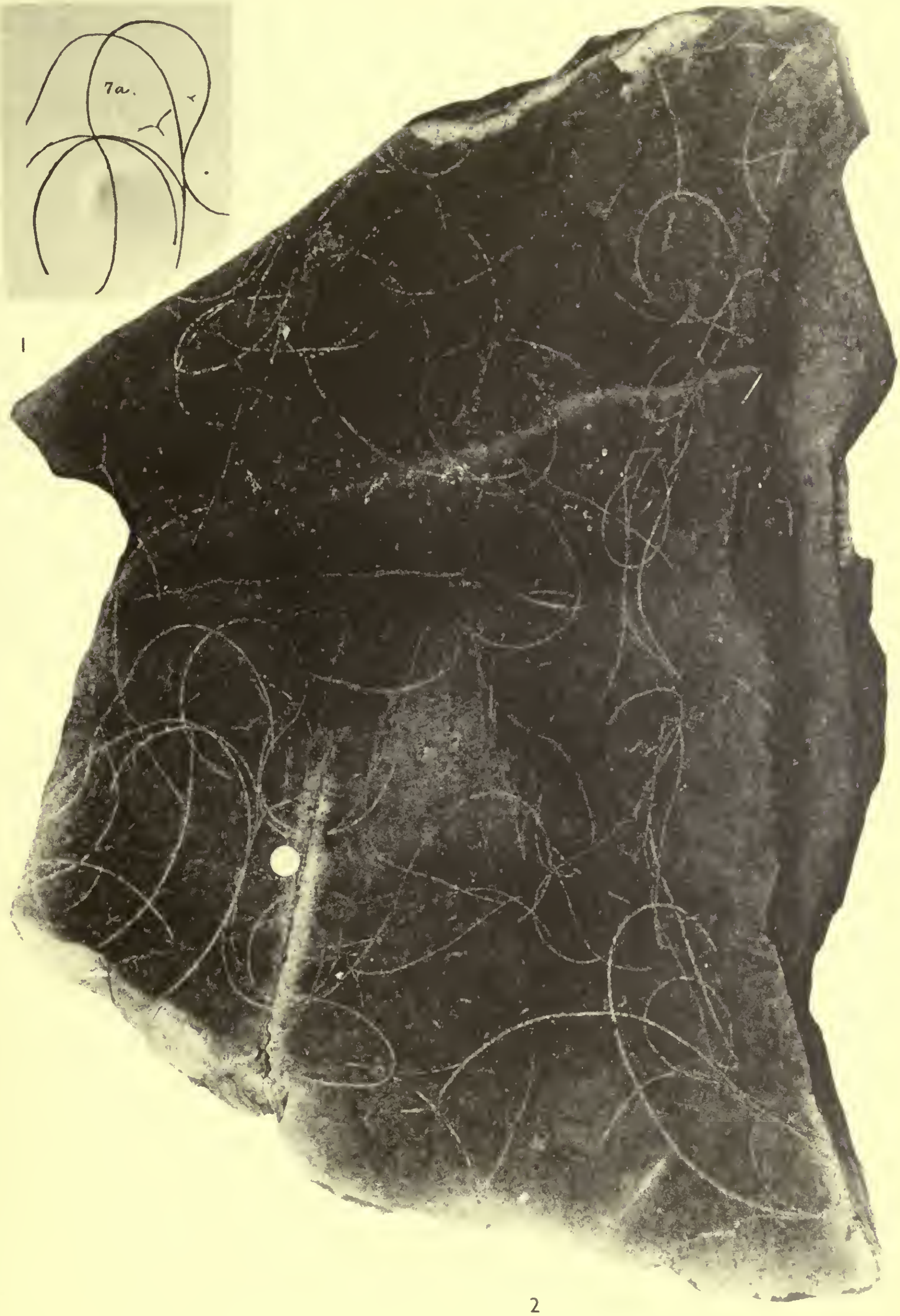

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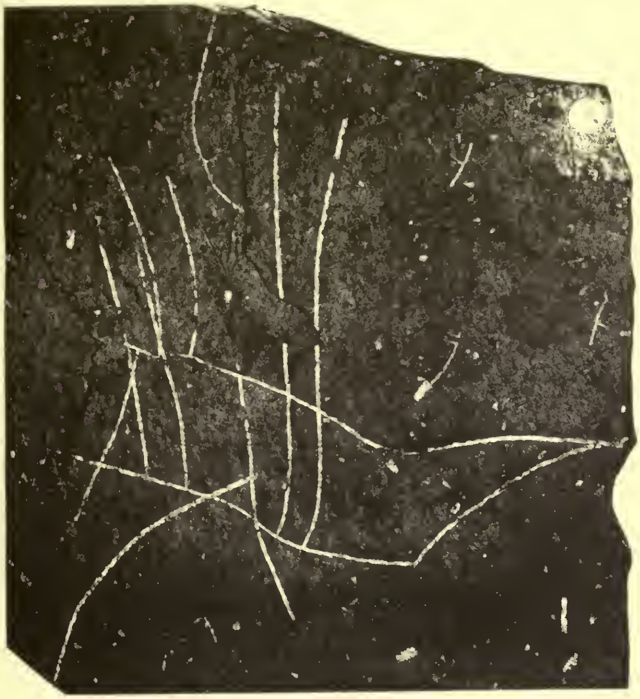
PLATE 2

Pleurograptus linearis (Carruthers)

FIG. 1. Holotype, Q.848, natural size. Hartfell Shales. Hartfell Spa.

FIG. 2. Copy of page from Carruthers' MS notes showing drawing of type slab and the original published figures (1858–59) half original size.

FIG. 3. Specimen figured by Nicholson, 1867, fig. 1, refigured Elles & Wood, pl. 16, fig. 7. Q.27, natural size. Hartfell Shales. Hartfell Spa.



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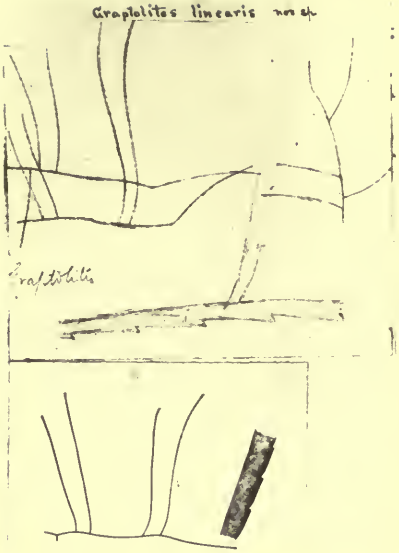

Graptolites linearis nov sp
Graptolites

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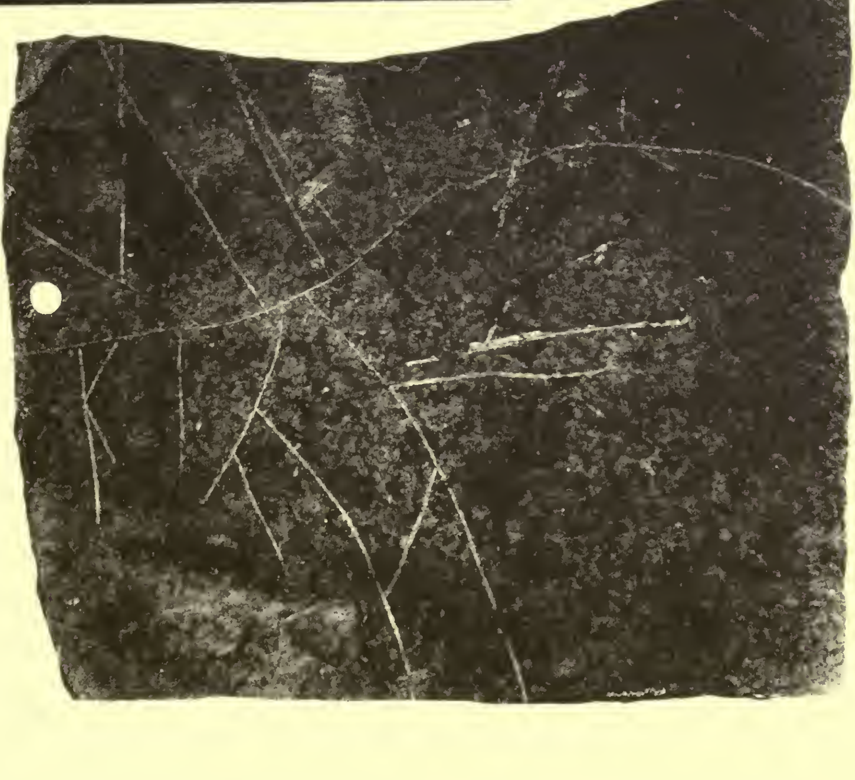

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PLATE 3

Dicellograptus elegans (Carruthers)

FIG. 1. Holotype, Q.850, natural size. Hartfell Shales. Hartfell Spa.

Dicranograptus clingani Carruthers

FIG. 2. Specimen figured Carruthers 1868, fig. 6b, Q.842, natural size. Hartfell Shales. Hartfell Spa.

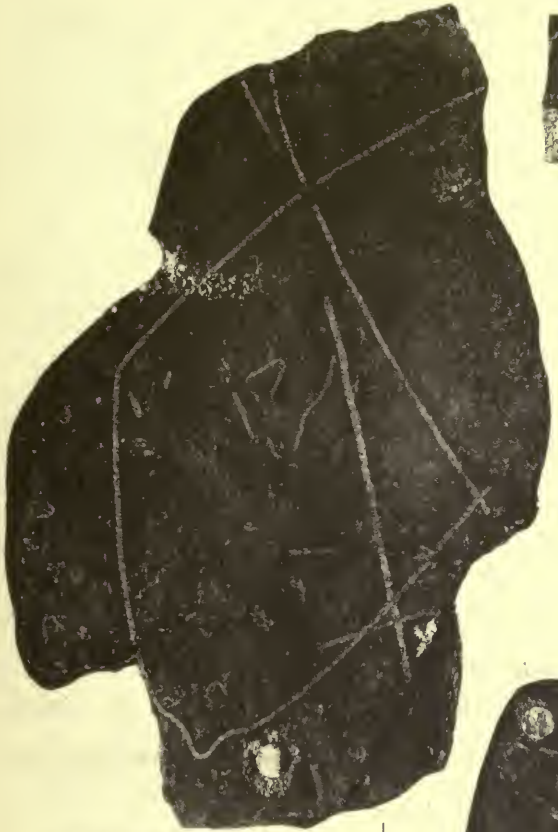
FIG. 3. Lectotype, Carruthers 1868, fig. 6a, refigured Elles & Wood, pl. 24, fig. 1a, Q.55, natural size. Hartfell Shales. Hartfell Spa.

FIG. 4. Same, × 5.

Dicellograptus moffatensis (Carruthers)

FIG. 5. Page from Carruthers' MS notes showing original drawings and copy of published figure (1858–59) half original size.

FIG. 6. Type slab, Q.843, natural size. The lectotype, figured by Elles & Wood, pl. 23, fig. 1a, is marked with the arrow. Hartfell Shales. Hartfell Spa.



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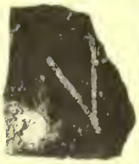

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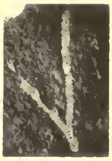

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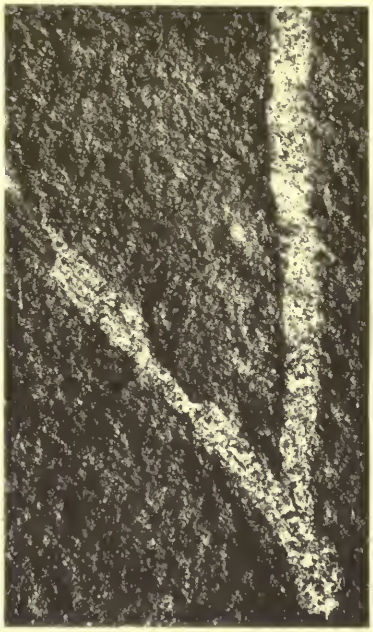

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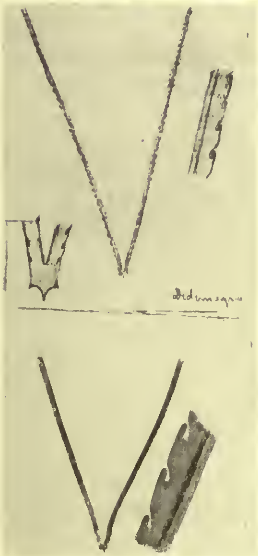

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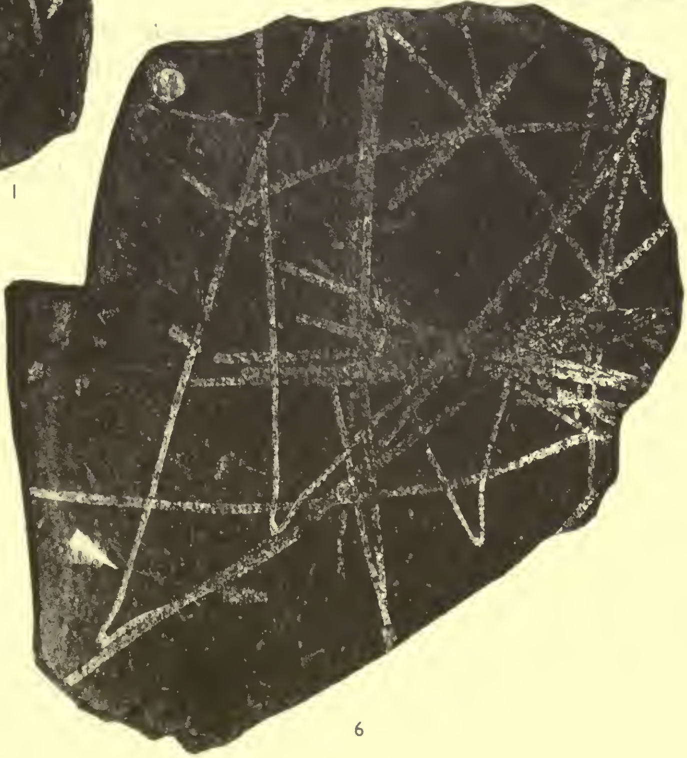

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PLATE 4

Climacograptus minutus Carruthers

FIG. 1. Lectotype, Q.80, ×5. Moffat, horizon and locality uncertain.

FIG. 2. Specimen figured Carruthers 1868, fig. 10b. Q.1372, as *C. minutus* but probably *C. scalaris miserabilis* E. & W. ×5. Moffat, horizon and locality uncertain.

Climacograptus minimus (Carruthers)

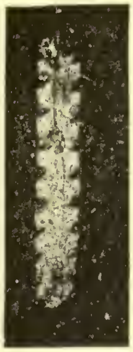
FIG. 3. Type slab, Q.82, natural size, showing poorly preserved biserial graptolites. Horizon and locality uncertain.

Cryptograptus tricornis (Carruthers)

FIG. 4. Slab with numerous specimens, Q.1299, lectotype marked with arrow, natural size. Hartfell Shales. Hartfell Spa.

FIG. 5. Drawings from Carruthers' MS notes showing the different appearances of the rhabdosome half original size.

FIG. 6. Copy of original figures (1858–59) half original size.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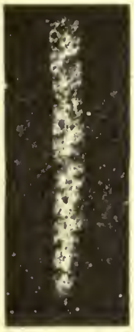
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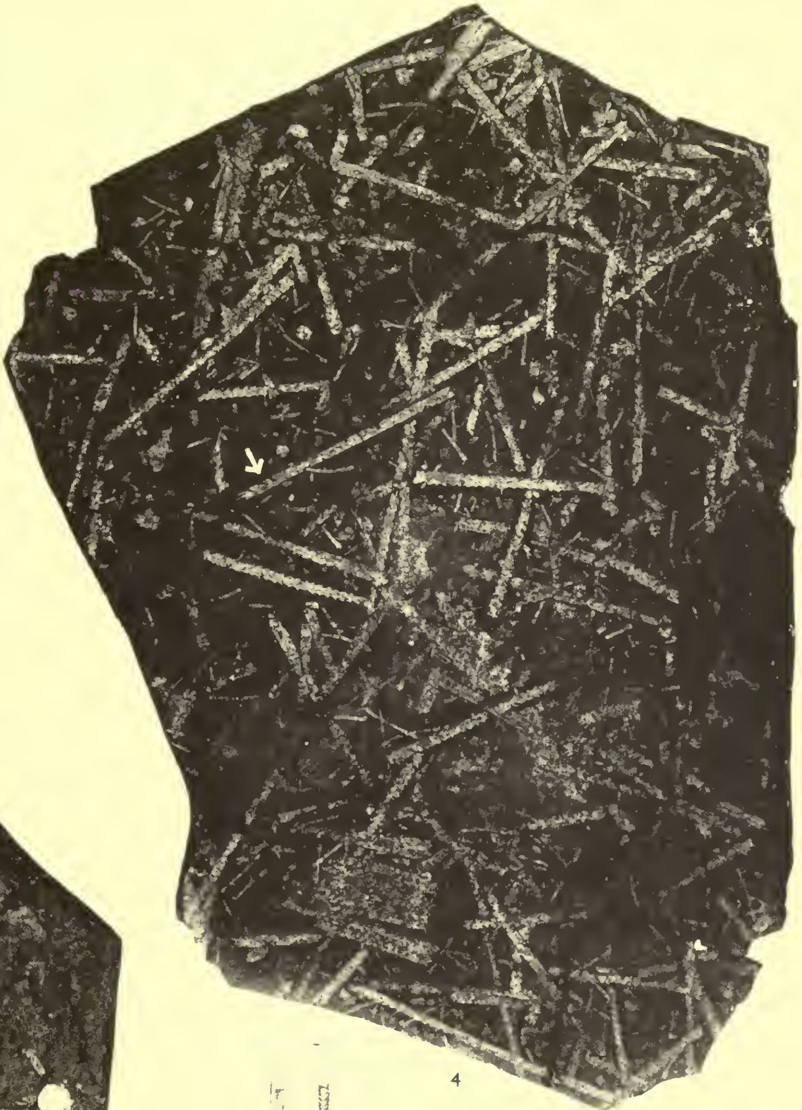
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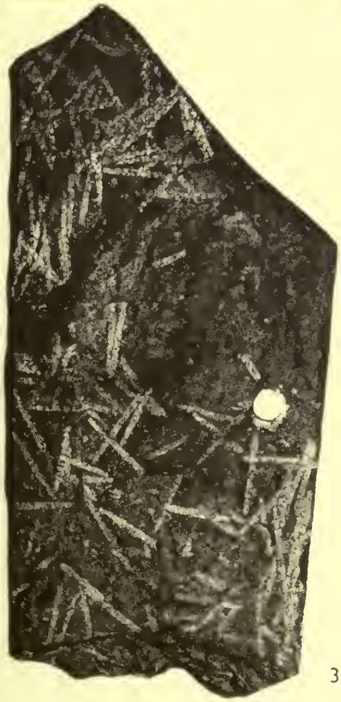
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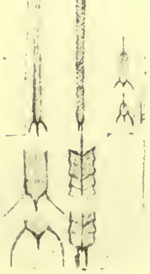
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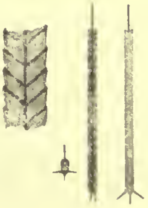
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PLATE 5

Monograptus clingani (Carruthers)

Fig. 1. Specimen showing distal part of the rhabdosome, BU 1667, figured Lapworth 1876, fig. 3a, refigured Elles & Wood, pl. 46, fig. 11d, natural size. Birkhill Shales. Dobbs Linn.

Figs. 2 and 4. Specimen figured Carruthers 1868, fig. 19b. Q.84, natural size and ×5. Moffat.

Figs. 3 and 5. Lectotype, figured Carruthers 1868, fig. 19a, Q.87, natural size and ×5. Moffat.

Monograptus intermedius (Carruthers)

Fig. 6. Holotype, Q.88, figured Carruthers 1868, fig. 18, natural size. Birkhill Shales. Moffat.

Rastrites maximus Carruthers

Fig. 7. Neotype, BU 1692, figured Elles & Wood, pl. 50, fig. 6b, × 2½. Upper Birkhill Shales. Riskinhope Burn, Yarrow.

Cyrtograptus murchisoni Carruthers

Figs. 8 and 9. Specimen and counterpart, GSM 10717–8, half natural size. These are the slabs from which Carruthers made his description and idealized figure. Wenlock Shales. Builth

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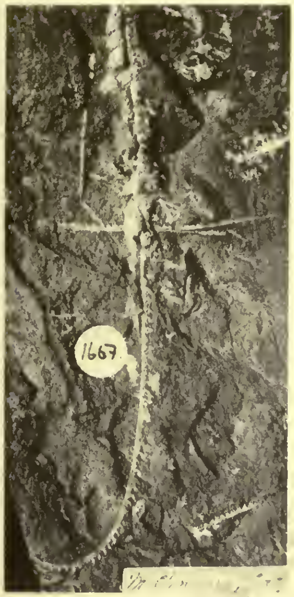

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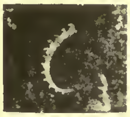

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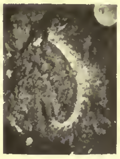

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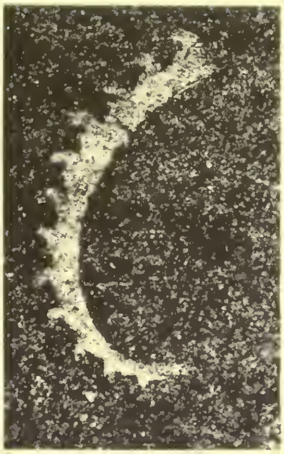

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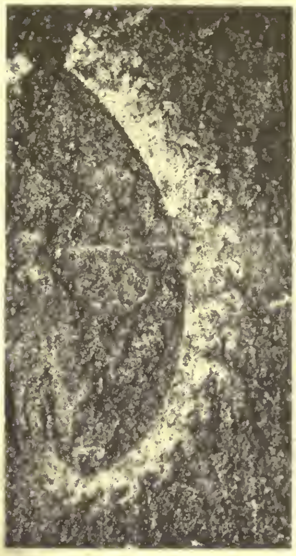

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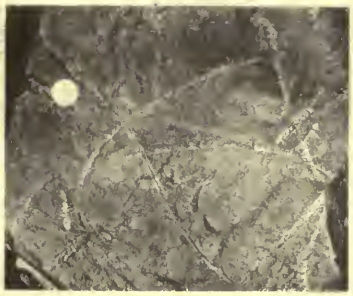

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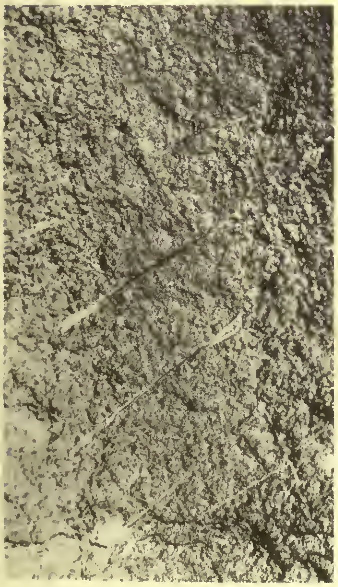

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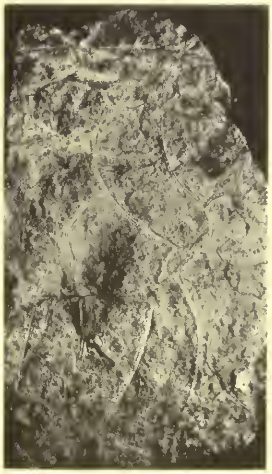

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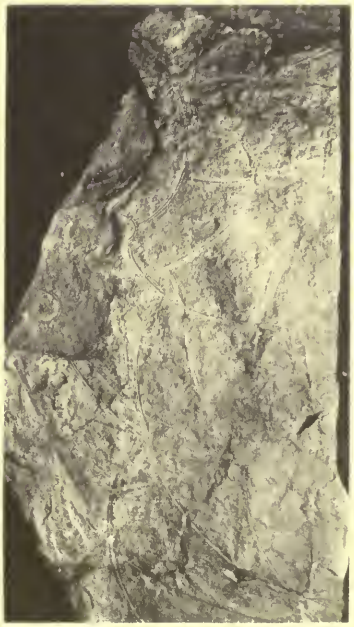

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PRINTED IN GREAT BRITAIN
BY ADLARD & SON LIMITED
BARTHOLOMEW PRESS, DORKING

A REVISION OF THE ENGLISH WEALDEN FLORA, I

CHARALES—GINKGOALES

J. WATSON

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
GEOLOGY Vol. 17 No. 5

LONDON: 1969

A REVISION OF THE ENGLISH WEALDEN FLORA, I

CHARALES—GINKGOALES

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*Pp.*207–254; 6 *Plates*; 64 *Text-figures*

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GEOLOGY Vol. 17 No. 5
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THE BULLETIN OF THE BRITISH MUSEUM (NATURAL HISTORY), *instituted in* 1949, *is issued in five series corresponding to the Departments of the Museum, and an Historical series.*

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World List abbreviation
Bull. Br. Mus. nat. Hist. (Geol.).

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A REVISION OF THE ENGLISH WEALDEN FLORA, I

CHARALES—GINKGOALES

By JOAN WATSON

CONTENTS

I. INTRODUCTION 210
II. SYSTEMATIC DESCRIPTIONS 214
  THALLOPHYTA 214
    CHLOROPHYCEAE 214
      CHARALES 214
        CIRCONITELLA gen. nov. 214
          Circonitella knowltoni (Seward) n. comb. . . 215
        GYROGONA Lamarck 217
          Gyrogona medicaginula Lamarck 217
  BRYOPHYTA 218
      MUSCI 218
          ? Bryophyte leaf 218
      HEPATICAE 218
        HEPATICITES Walton 219
          Hepaticites zeilleri (Seward) n. comb. . . . 219
          Hepaticites ruffordi sp. nov. 220
        THALLITES Walton 220
          Thallites valdensis (Seward) n. comb. . . . 221
          Thallites catenelloides (Seward) n. comb. . . . 223
  PTERIDOPHYTA 224
      LYCOPODIALES 224
        SELAGINELLA 224
          Selaginella dawsoni (Seward) 224
      EQUISETALES 227
        EQUISETITES Sternberg 227
      FILICALES 228
        MATONIACEAE 228
        MATONIDIUM Schenk 228
          Matonidium goepperti (Ettingshausen) 228
        DIPTERIDACEAE 228
        HAUSMANNIA Dunker 228
          Hausmannia dichotoma Dunker 228
        SCHIZAEACEAE 229
        RUFFORDIA Seward 229
          Ruffordia goepperti (Dunker) 229
        PELLETIERIA Seward 232
          Pelletieria valdnensis Seward 232
        POLYPODIACEAE 235
        ASPIDISTES Harris 235
          Aspidistes sewardi sp. nov. 236

Unclassified ferns 237
CLADOPHLEBIS Brongniart 237
Cladophlebis longipennis Seward 237
Cladophlebis albertsii (Dunker) 237
Cladophlebis browniana (Dunker) 238
Cladophlebis dunkeri (Schimper) 238
SPHENOPTERIS Sternberg 238
Sphenopteris ruffordi (Seward) n. comb. 238
Sphenopteris fittoni Seward 238
Sphenopteris fontainei Seward 238
LECKENBYA Seward 238
Leckenbya valdensis (Seward) 238
TEILHARDIA Seward 238
Teilhardia valdensis Seward 238
ONYCHIOPSIS Yokoyama 238
Onychiopsis psilotoides (Stokes & Webb) . . . 238
WEICHSELIA Stiehler 239
Weichselia reticulata (Stokes & Webb) 240
Spermatophyta 240
Pteridospermae 240
PACHYPTERIS Brongniart 240
Pachypteris lanceolata Brongniart 240
Gymnospermae 242
Cycadales 242
NILSSONIA Brongniart 242
Nilssonia schaumburgensis (Dunker) 242
BECKLESIA Seward 244
Becklesia anomala Seward 244
Becklesia sulcata sp. nov. 247
Ginkgoales 248
PSEUDOTORELLIA Florin 248
Pseudotorellia heterophylla sp. nov. 248
III. References 251

SYNOPSIS

The English Wealden flora described by Seward (1894, 1895) is here revised using modern techniques, in particular in the study of the plant cuticles. Much of the work has been carried out on the existing collections in the British Museum (Natural History), but a number of new species in the form of isolated leaf cuticles have been obtained by bulk maceration of " coaly-shales " collected by the author from the Fairlight Clay at Hastings, Sussex.

The present work covers the Thallophyta, Bryophyta, Pteridophyta, Pteridospermae, Cycadales and Ginkgoales. A second part will deal with the Bennettitales and Coniferales together with a special section devoted to a complete revision of the Wealden Equisetales.

I. INTRODUCTION

English Wealden Flora.

This work is a revision of part of the English Wealden Flora, using modern techniques. It has been carried out largely from a study of the Wealden plants in the British Museum (Natural History). Most of this material was collected from the coast in the neighbourhood of Hastings, Sussex in the latter part of the last century and belongs to the Beckles, Dawson, Mantell and Rufford Collections. The majority was collected by Mr. P. Rufford but unfortunately his specimens are merely labelled " Ecclesbourne, Nr. Hastings " and the exact localities are not recorded. Attempts were made to find fresh material along the coast between Hastings and Pett Level but unfortunately no fossils were found. However, material was obtained from coaly lenses and partings which occur in the Hastings Beds. Bulk maceration of these " coaly-shales " yielded quantities of spores, isolated leaves and even small shoots. Two of the species thus obtained are described here, including the first record of a member of the Ginkgoales from the English Wealden. Similar coaly-shales from the Wealden in the Isle of Wight yield identical plant fragments.

The flora was previously described by Seward (1894, 1895). His identifications of the fossils were based solely on macroscopic features and were figured by means of woodcuts and lithographs. A re-examination of the fossils using modern techniques shows that many of Seward's determinations are wrong. However, where the type material of a particular species (usually from the German Wealden) has not been redescribed or examined it is impossible to say if the identification is truly accurate.

Seward arranged the flora into about seventy-five species. From more than a dozen of these I was unable to get any significant new information, and unless better material is found it seems that only a redescription of their gross morphology would be possible. Most of the ferns come into this category and only a few species are dealt with here in any detail. There are very few fertile specimens available and one such fern, *Onychiopsis psilotoides* (Stokes & Webb), has recently been redescribed by Tattersall (1961). The practice of coating specimens with varnish in the past has caused the destruction of the cuticle in many specimens and has greatly hindered revision.

The Thallophyta, Bryophyta, Pteridophyta, Pteridospermae, Cycadales and Ginkgoales are described in this paper with the exception of the Equisetales. A recent find of more petrified material belonging to the Equisetales renders necessary a further revision of the species (see Watson 1964), and this will be published in a later volume together with the Bennettitales and Coniferales.

Other Wealden Floras

The Wealden floras of Germany, France and Belgium were all described in the last century in the same way that Seward described the English flora. Since then little progress has been made and work as detailed as that presented here scarcely exists. Cuticles have been described for a few species from time to time (Carpentier 1939) but the amount of work to be done remains enormous. The German Wealden flora in particular should be thoroughly revised as it contains so many type specimens. A number of English fossils are referred to German species merely on external characters. When a species under revision can only be compared with the inadequate, original nineteenth century description of the type an impossible situation arises. It has hitherto been thought that the English and German floras are more or less identical but I suspect that this may not be so. In some cases fairly recent work on foreign material has shown that a number of English specimens previously referred to German species are different from the type [*Sphenolepis kurriana* (Dunker), *Sphenolepis sternbergiana* (Dunker), *Pseudocycas dunkeriana* (Schenk)] and these were described as new species (Watson 1964). But for the vast majority of species no such comparison is possible. It is also now known that the German and English Wealden are not wholly contemporaneous (see Table I). For these reasons I feel that it is of little value to produce comparative lists of species for the various localities. This has been done frequently in the past and perhaps most recently and comprehensively by Delcourt & Sprumont (1955). Such lists, however, are probably highly inaccurate and will remain so until there is a wholesale revision of all Lower Cretaceous fossil floras.

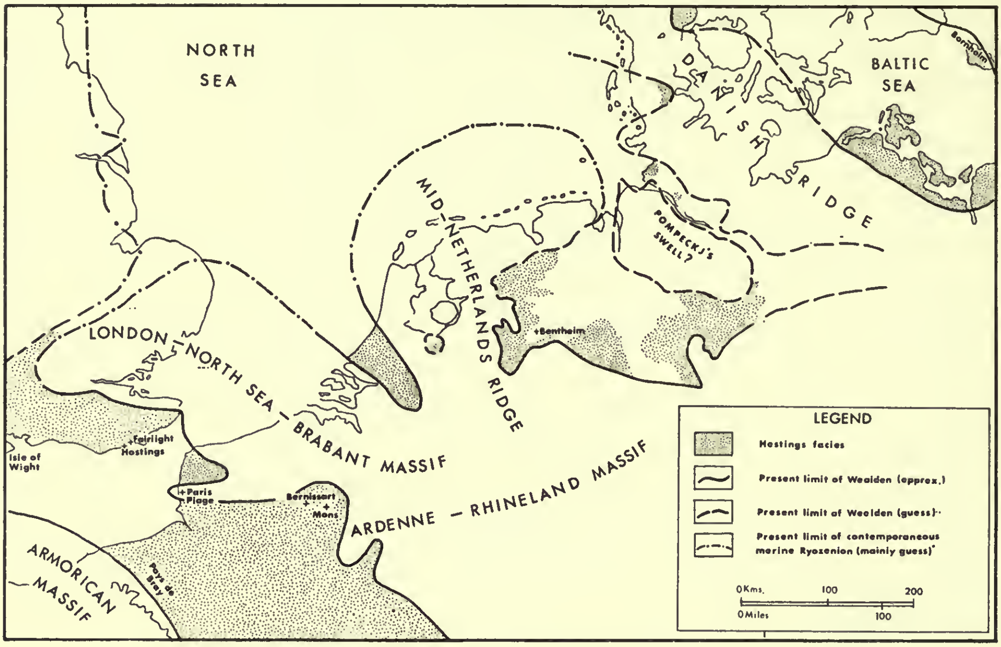

NORTH SEA
BALTIC SEA
Bornholm
DANISH RIDGE
MID-NETHERLANDS RIDGE
POMPECKJ'S SWELL?
Bentheim
LONDON – NORTH SEA – BRABANT MASSIF
ARDENNE – RHINELAND MASSIF
ARMORICAN MASSIF
Isle of Wight
Fairlight
Hastings
Paris Plage
Bernissart
Mons
Pays de Bray
LEGEND
Hastings facies
Present limit of Wealden (approx.)
Present limit of Wealden (guess)
Present limit of contemporaneous marine Ryazanian (mainly guess)
0 Kms.
100
200
0 Miles
100

FIG. 1. Inferred present extent of Wealden strata. (After Allen 1967)

Techniques

Techniques used were of the simplest. With few exceptions the usual method for bulk macerations was used (see Harris 1926).

Stratigraphical background

The stratigraphy of the Wealden has been described by White (1928), Allen (1954, 1955, 1959, 1960, 1965, 1967), Hughes (1958) and Howitt (1964). Owing to its alleged relict fauna and flora of Jurassic affinity the English Wealden has on occasions been assigned to the Jurassic System. It is now, however, generally

	TETHYAN	BOREAL			
	South-east France	North-west Germany		Southern England	
CRETACEOUS (part)	Barremian	Barremian		Weald Clay	CRETACEOUS (part)
	Hauterivian	Hauterivian			
	Valanginian	'Upper & Middle Valdensis'		Hastings Beds	
	Berriasian	'Wealden'			
		Upper Serpulite	PURBECK	Durlston Beds	
		Lower Serpulite		Lulworth Beds	JURASSIC (part)
		Münder Marls		Portland Beds	
JURASSIC (part)	Tithonian	Eimbeckhausen Plattenkalk			

TABLE. 1—Correlation of N. W. European " Wealden " (from table 4 in Dodson, Rex, Casey & Allen 1964).

accepted as part of the Cretaceous. Part, or even all, of the Purbeck might also be Cretaceous. Table I is a correlation table for the Wealden of north-west Europe recently proposed by Dodson, Rex, Casey & Allen (1964). On the basis of glauconite studies the radiometric age of the Jurassic/Cretaceous boundary is estimated to be about 135 million years. Text-fig. 1 shows the present extent of the Wealden.

The Fairlight Clays have yielded most of the fossil plants, particularly in the region of Ecclesbourne Glen. The large number of specimens collected by Mr. P. Rufford and others has led to the false impression, which has been perpetuated (Gallois 1965), that plants are abundant in the Fairlight Clays. This is not so: even small fragments are quite rare. It has not been possible to ascertain the exact localities and horizons at which Rufford collected; nor is it known over what period of time the collection was assembled. In a brief description of the Hastings Beds by Rufford (Seward 1894 : xvii) he refers to the Fairlight Clays " yielding, very locally, Ferns, Cycads and Conifers " and also to " the very limited extent of outcropping fossiliferous strata ". In the early years of this century (around 1910) a further important collection of Wealden plants was made by P. Teilhard de Chardin and Felix Pelletier, two Jesuit priests who stayed in the area for four years. Their specimens (Seward 1913) were collected mainly in the neighbourhood of Fairlight which is about a mile to the east of Ecclesbourne Glen. The collection was subsequently divided between the British Museum (Natural History) and the Hastings Museum. The Hastings Museum also has a large number of Rufford's specimens, many of which are the counterparts of the specimens in the British Museum (Natural History). Attempts at collecting in recent years have yielded nothing to compare with the magnificent specimens (fronds three feet long) obtained by these earlier collectors.

Acknowledgements

This work forms part of a Ph.D. thesis of the University of Reading, supervised by Professor T. M. Harris, F.R.S. and I thank him for his unfailing patience, kindness and encouragement. I wish also to thank Professor P. Allen for much help and for permission to reproduce his text-figures.

Some of the work was carried out in the Department of Palaeontology, British Museum (Natural History), some in the Botany Department, University of St. Andrews and some in the Herbarium, Manchester Museum where I was given research facilities for which I am most grateful. Thanks are due to the Keeper of Palaeontology, British Museum (Natural History) for permission to work on the collections.

Tenure of a D.S.I.R. Studentship is gratefully acknowledged.

II. SYSTEMATIC DESCRIPTIONS

Unless otherwise indicated in the text all specimens are in the collections of the British Museum (Natural History) and are prefixed by V.

THALLOPHYTA

CHLOROPHYCEAE. CHARALES

Organ Genus *CIRCONITELLA* nov.

Diagnosis. Gyrogonite uncalcified, cutinised; surrounded by five sinistrally spiralled cells; shape ellipsoidal, circular in transverse section. Apical pole formed by all five cells; basally ending against a basal plate; without basal cage.

Type species. *Chara knowltoni* Seward 1894; 13, Text-fig. 1.

Discussion. This genus is recognized for the type species which was formerly included in *Nitellites* Horn af Rantzien in my Ph.D. thesis of 1964. The diagnosis of *Nitellites*, however, requires that size and shape should be very close to that of the

Recent genus *Nitella* but *C. knowltoni* differs in being somewhat larger and unflattened.

Dijkstra (1959) describes an uncalcified gyrogonite which he refers to as "*Praechara symmetrica* Peck cf.". I am satisfied, from his diagnosis and photographs that this fossil is identical with *C. knowltoni* (Seward). Whilst this species fits into *Praechara* Horn af Rantzien (1954) on its general shape and apical structure, *Praechara* has hitherto been used only for members of the Characeae, i.e. calcified gyrogonites which cannot be placed in other well-defined genera.

Circonitella knowltoni (Seward) comb. nov.

Pl. 1, figs. 1–5; Text-figs. 2–6.

1894 *Chara knowltoni* Seward : 13, text-fig. 1.
1959 *Praechara symmetrica* Peck cf.; Dijkstra : 15, pl. 2, figs. 20–23.

EMENDED DIAGNOSIS. Gyrogonite uncalcified, ellipsoidal in side view, apical and basal halves similar, 400μ to 665 μ long and 380 μ to 550 μ wide. Spiral cells five, sinistrally spiralled, about 45 μ wide near equator and showing about twelve convolutions laterally. Cells usually slightly concave with distinct intercellular ridges 3 μ to 15 μ wide, sometimes flat and occasionally convex. Outer cutinised membrane (ectosporostine of Horn af Rantzien) marked with coarse but very low and ill-defined tubercles up to 5 μ diameter. Inner membrane (endosporostine of Horn af Rantzien) present, delicate and without a patterned surface. Apical pole formed by ends of spiral cells meeting in a slightly eccentric pattern; basal pole with rounded plate 100 μ wide; no cage or basal claws present.

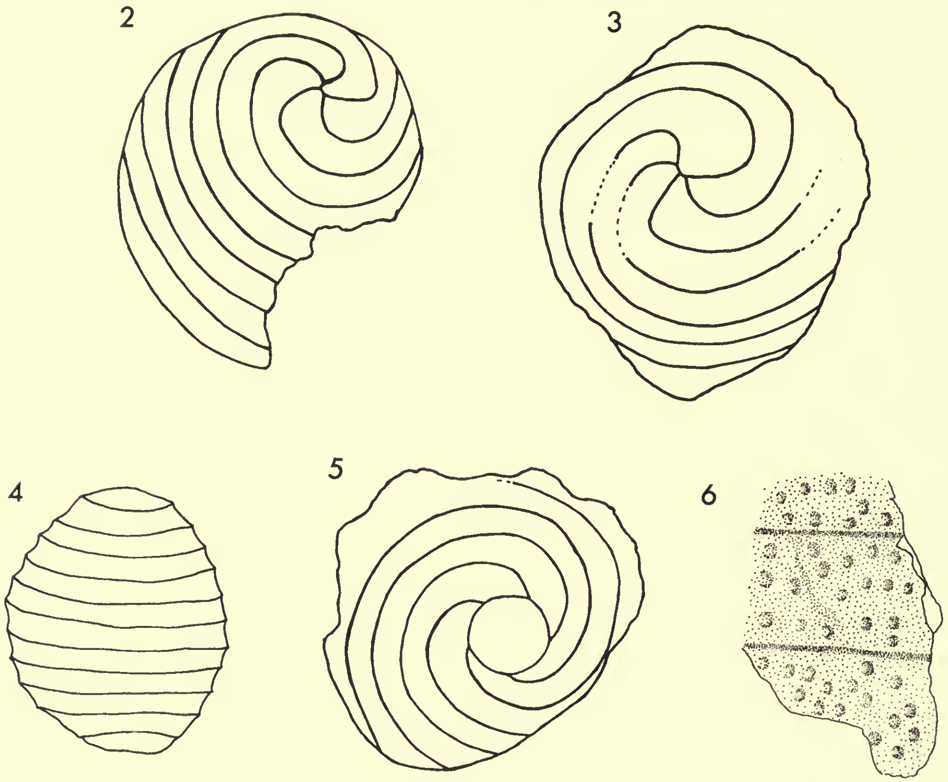
NEOTYPE. V.51555.

DESCRIPTION. Numerous black cutinized gyrogonites are embedded in an argillaceous matrix, the majority being flattened and presenting a lateral view but a few being orientated so as to show polar views. A few gyrogonites preserved by pyritization are completely unsquashed and were obtained by macerating small pieces of the rock in water. These specimens show that the gyrogonite was originally completely circular in section and that flattening occurred during preservation. Whereas most of the flattened specimens have concave spiral cells with intercellular ridges the solid ones have convex spirals with depressions between and tend to be somewhat larger. However, one of them (V.51555) has part of the convex surface broken away revealing the familiar concave cells with ridges below. These two surfaces are interpreted as the outer and inner walls of the spiral cells.

Apical poles are not seen nearly so frequently as basal poles but a few undistorted specimens were obtained. It may be noted that in the material from the Netherlands, Dijkstra (1959) also found the apical poles of the gyrogonites less well preserved. The tips of the spiral cells tend to be swollen and meet in a slightly irregular pattern. Many more basal poles are seen with the easily identifiable circular plate against which the five spiral cells end in a regular manner. Their width near the pole is the same as at the equator.

Laterally up to twelve convolutions of spiral cells are seen each making more than two turns. Thus the spiral is so flat that the furrows and ridges appear almost horizontal. As mentioned above the spiral cells are concave in most gyrogonites but convex in a few specimens. There are also many in which they are flat and their margins are then nearly, or quite, invisible in the untreated fossil. For variety in intercellular ridges compare Pl. 1, figs. 2, 4.

The tubercles on the ectosporostine are irregularly arranged about 8 μ apart, usually about four tubercles across the width of a spiral cell. Many gyrogonites gave no satisfactory cuticles at all and some that did yield cuticles were less clearly marked. The cuticle is usually reddish-brown in colour but in parts the inner membrane of the wall is seen alone as a straw-coloured homogeneous layer without markings of any kind. The coronula is not known, nor is the oospore.



Figs. 2–6. *Circonitella knowltoni* (Seward). 2, 3. Gyrogonites showing apical pole. Fig. 2, specimen accidentally destroyed. Fig. 3, V.51549. × 100. 4. Side view of a gyrogonite with concave cells, showing the very flat spiral. V.51550. × 75. 5. Basal pole of a gyrogonite. V.3114. × 100. 6. Cutinized wall showing part of three spiral cells with tubercles on the outer layer. The inner layer of the wall is seen on the right of the middle cell. Slide V.51551. × 350.

Dijkstra suggested that his fossils were originally calcified but became decalcified during preservation. It is much more likely, however, that the present specimens were never calcified. There is evidence that both the concave inner wall and the convex outer wall of the gyrogonite cells are composed of organic matter and if my interpretation of these layers is correct then it seems conclusive. It is clear that in the specimens with only the inner organic layer present the fine clay matrix is everywhere pressing against this layer; there is no gap at all such as would be left if a lime-shell had been dissolved. We would have to suppose that decalcification occured first, then preservation. This species is preserved in a unique way in specimens from two widely separated localities and it seems unlikely to have been caused by the same unusual event at two distant places.

The absence of a calcareous shell on the outside of the gyrogonite immediately suggests Nitellaceous affinities but further study shows that in other features it is more like the Characeae. I make no assumption about the correct classification of the plant producing this gyrogonite.

In all the Nitellaceae the gyrogonites are laterally compressed whereas *Circonitella knowltoni* is quite round in transverse section as are members of the Characeae. In studying a number of living Nitellaceae, Horn af Rantzien (1959) found *Nitella hyalina* to be the least flattened, a typical specimen being 340 μ long, 260 μ wide and 180 μ thick. He also gives details concerning the average size of *Nitella* gyrogonites: '. . . generally speaking the oosporangia (gyrogonites) of *Nitella* are small, in most species the length does not exceed 350 μ'. *C. knowltoni* is much larger, attaining almost twice this length, although *Nitella* gyrogonites with larger dimensions do occur, e.g. *N. flexilis* which reaches 575 μ long (Groves & Bullock-Webster 1917).

Twelve convolutions of spiral cells seen in lateral view is common in the Characeae but in the genus *Nitella* the largest number known is eleven, in *N. polygyra*. A more usual number in this group is five or six and hence the angle of the spiral is steeper than in *C. knowltoni*.

Amongst British Charales the most similar ectosporostine pattern is seen in *N. opaca*, although the tubercles are more numerous and larger. Most of the Characeae have a much smoother granulate surface. The absence of basal claws accords with Recent species of *Nitella*.

Apart from Quaternary fossils the only other uncalcified gyrogonites are *Nitellites sahnii* Horn af Rantzien and *Nitellites* sp. (Horn af Rantzien 1957) from the Middle to Upper Jurassic Rajmahal series of India. Both differ from *C. knowltoni* in having more in common with the Recent genus *Nitella*. They are much smaller, being only 160 μ at the longest, and they are laterally compressed. The spiral cells show only six to eight convolutions and the ectosporostine has a reticulate surface.

Genus ***GYROGONA*** Lamarck

Gyrogona medicaginula Lamarck

Selected references-

1804 *Gyrogona medicaginula* Lamarck : 355.
1829 *Chara medicaginula* (Lamarck); Lyell : 91, pl. 13, figs. 1–8.
1933 *Gyrogona medicaginula* Lamarck; Groves : 24, 25, 39.
1965 *Gyrogona medicaginula* Lamarck; Grambast & Paul : 239, pl. 1, figs. 1–4.

Remarks. Several gyrogonites of this species are present in a piece of pure siliceous rock (V.2928) which is included in the Wealden Collections (British Museum, Natural History). The specimen has the appearance of a large pebble from the beach and it seems probable that it is not Wealden in age. *G. medicaginula* is otherwise only known from the Tertiary (Lyell 1829, Grambast & Paul 1965) and is found in the Oligocene of the Isle of Wight. The specimen is accompanied by a note written by Groves and is probably the specimen to which he refers (Groves 1933 : 25) when saying " Fruits collected from a Wealden deposit, Fairlight Glen, Hastings (Sussex), England . . . are considered by the present writer to be referable to this species ".

The matrix cannot be matched to anything in the Hastings Beds and the gyrogonites of *G. medicaginula* are much larger than is usual in pre-Tertiary species. It seems probable, therefore, that the specimen was mistakenly identified as Wealden; perhaps washed-up on the beach near Hastings.

BRYOPHYTA

MUSCI

? ***Bryophyte*** leaf.

Text-figs. 7–9

Leaf elliptical, nearly 2 mm. long, just over 1 mm. wide. Margin entire, one end (possibly both) rounded. No midrib present. Lamina flat, one cell thick, cells forming about eight longitudinal rows, marginal cells smaller, about as long as broad. Cell walls thin, not locally thickened at corners; no surface thickenings observed.

Material. V.2857, V.2857*a*, V.2857*b*.

This small fossil is known from three isolated specimens which are very similar; one has a counterpart. The above description assumes it is like a Bryophyte leaf but I have been unable to find a Bryophyte leaf with similarly arranged cells. In the leafy liverworts the cells tend to be isodiametric or rounded and do not form longitudinal rows. In *Naiadita lanceolata* Buckman (Harris 1938) the cell rows are markedly transverse. In the mosses they are isodiametric to elongated but they may form longitudinal rows. Transversely elongated cells are very rare in mosses but they are seen in a few *Tortula* species. However they have leaves which are otherwise different.

Ventral scales and rounded appendages of the scales of the Marchantiales have more or less elongated cells and where rows are recognizable they are transverse, never longitudinal. In fern ramenta the cells are often in longitudinal rows but are usually very narrow.

HEPATICAE

The fossils described here are all thalloid and branch dichotomously and some of them form a rosette-like growth. Some show definite Hepatic features rather than Algal, but others do not, although they look like Hepatics. Various generic names have been used for such fossils by earlier authors (e.g. *Marchantites* Brongniart) suggesting rather precise affinity. Walton (1925) in giving fine details of such fossils for the first time revised their classification. A fossil with definite Hepatic features he called *Hepaticites*. This feature in practice is usually the presence of rhizoids. Fossils in which no rhizoids were demonstrated he called *Thallites*. According to this scheme the genus *Marchantites* is now restricted to forms showing definite Marchantialean characters. Thus *Marchantites zeilleri* Seward was referred to the genus *Thallites* Walton (Harris 1942). Further study of this plant has revealed the presence of rhizoids and it is here included in *Hepaticites* Walton.

Lundblad (1954) separated from *Hepaticites* those species showing Marchantialean ventral scales as *Marchantites* and those with Marchantialean air-chambers as *Marchantiolites*. In the present work the two genera of Walton suffice, but one species which almost certainly has Marchantialean ventral scales would have been placed in *Marchantites* had it been well enough preserved for the facts to be secure.

Genus ***HEPATICITES*** Walton 1925 : 565

Hepaticites zeilleri (Seward) comb. nov.

Pl. 2, figs. 1–3

1894 *Marchantites Zeilleri* Seward : 18, pl. 1, fig. 3.
1942 *Thallites zeilleri* (Seward) Harris : 397.
1954 *Thallites zeilleri* (Seward); Lundblad : 408.

EMENDED DIAGNOSIS. Plant thalloid, dichotomously branched, distance between dichotomies not constant. Thallus about 3 mm. broad, composed of dark, well defined midrib 1 mm. wide and delicate lamina probably one cell thick. Margins entire. Cells of thallus in rows, longitudinal in midrib but inclined at an angle of about 45° in lamina; cells about 30 μ wide. Near apex midrib tending to divide into number of divergent dark bands separated by thinner tissue. Numerous unicellular thin walled, non-tuberculate rhizoids arising on midrib, up to 5 mm. long and typically 40 μ wide.

HOLOTYPE. V.2330.

DESCRIPTION. The holotype suggests a rosette shaped thallus in the position of growth (Pl. 2, fig. 1 shows the counterpart). A second specimen shows smaller pieces of thallus mixed with fragments of *Onychiopsis* and is more likely to have been deposited by water.

The thallus branches are delicate towards the tip and the apex is nowhere visible. Here the midrib is more delicate and seems to divide. In this delicate part longitudinal rows of cells can be seen but elsewhere the midrib is very dark and opaque and presumably several cells thick. The rows of cells in the lamina are clearly seen only in a few places and then only the longitudinal walls are preserved.

There is nothing suggesting Marchantialean air chambers or ventral scales. The rhizoids although clear are only moderately well preserved, unbranched and without septa; their walls appear to be plain rather than tuberculate. They form groups arising from the midrib and usually point forwards. A number of detached rhizoid bunches are present beside the thallus.

COMPARISON. *H. zeilleri* is the only British Wealden liverwort with a clearly defined midrib and lamina. Among other fossils it bears a most striking resemblance to *H. laevis* Harris (1931) from the Lower Lias of East Greenland. The rows of cells in that species are more clearly defined and the midrib is 0·5 mm. wider than in *H. zeilleri* but otherwise they look the same.

Other similar species are: *H. arcuatus* (Lindley & Hutton) Harris (1942 : 394, 1961 : 7) which is of similar dimensions and has a well defined midrib, but the lamina is three cells thick, and there are fewer rhizoids. *Thallites yabei* (Kryshtofovich 1932, 1938, Oishi 1940, Harris 1942) is a larger plant of which no microscopic details are known.

CLASSIFICATION. *H. zeilleri* looks very like *Pellia* and agrees with it in the cell-rows of the lamina and in the rhizoids. Plants of the *Pellia* form are familiar in the Jungermanniales anacrogynae but scarcely occur in other groups and accordingly *H. zeilleri* is placed here.

Hepaticites ruffordi sp. nov.

Pl. 2, figs. 4, 5

DIAGNOSIS. Thallus branched dichotomously at intervals of about 1 cm., width about 3–4 mm. Margins entire, apex probably notched. Greater part of thallus marked with grooves (considered to be ventral scales) at intervals of 0·5 mm. Grooves strongly arched, longitudinal in middle region but curving outwards and then slightly backwards at their ends. Middle region of older part of thallus, about 2 mm. wide, marked by two lines appearing thicker and beyond which grooves do not extend.

HOLOTYPE. V.2343.

DESCRIPTION. The only specimen known is preserved as an impression in fine sandstone; a little of the plant substance remaining as a dark stain but this has cracked and no cells are seen satisfactorily. Faint marks crossing the grooves may be the impression of cells but there is nothing more. No rhizoids were seen nor any structure in the lamina. *H. ruffordi* is tentatively placed in *Hepaticites* because it is thought to show a distinctive Hepatic character—ventral scales—even though rhizoids are not preserved. These ribs, or ventral scales, are of interest since they are confined to the Marchantiales. Unfortunately the specimen is too poorly preserved to be sure that they are indeed scales. I have, therefore, refrained from including it in *Marchantites* in Lundblad's sense.

COMPARISON. *Marchantites hallei* Lundblad (1955) is a liverwort from the Lower Cretaceous of Patagonia. It is similar in dimensions to *H. ruffordi* but is known in much more detail, having two sorts of rhizoids and well preserved ventral scales. *Hepaticites haiburnensis* Harris (1961 : 9) is another similar form in which the thallus extends further beyond the scales.

Genus ***THALLITES*** Walton 1925 : 564.

For discussion of *Thallites* see p. 219. The two species described here are associated in considerable numbers on certain bedding planes. Seward placed them in

Algites thinking them to be marine red algae. Closer study shows that they are more likely to be terrestrial liverworts though proof is lacking. They are certainly not marine for the rocks in which they occur are of purely freshwater origin and indeed the specimens are crowded with the small freshwater lamellibranch, *Neomiodon*. Despite careful study the two forms described here show so few details that they can hardly be considered to be properly characterized species. However, they have been described as such and as their names are fairly well known they are here retained.

Thallites valdensis (Seward) comb. nov.

Text-figs. 12–15

1894 *Algites valdensis* Seward : 4, pl. 1, figs. 1, 2.

Emended diagnosis. Plant thalloid; thallus forming rosette of segments branching dichotomously three or four times. Diameter of whole thallus up to 5·5 cm.; width of branches typically 4–5 mm., branches ending bluntly. Midrib represented by median dark line 100 μ wide and dichotomizing 5 mm. behind dichotomy of thallus. Cells in midrib region not differing from rest of lamina. Dark ribs passing obliquely across lamina at intervals of about 300 μ. Lamina apparently composed of one layer of thin walled cells ranging in size from about 15–75 μ.

Holotype. V.2857.

Description. Seven specimens were examined on three blocks of fine-grained calcareous sandstone. The preservation is poor and splitting of the rock has resulted also in splitting of the fossil into two parts. The rosette of branches strongly suggests that the plant has been preserved in position of growth. It accords with a suggestion made by Walton (1949) for a Carboniferous thallus which he called cf. *Hepaticites*. Like Walton's specimen there are several very perfect rosettes and it looks as though the central and oldest part of the thallus had decayed away before the plants were buried and preserved. Fragments would be unlikely to drift together into a neat rosette.

The general appearance of the cells is constant throughout the whole thallus though they vary considerably in size and shape. They are on the whole thin walled but additional organic material is present which tends to conceal their walls. The positions of the median line of the thallus and the ribs are merely marked by a greater concentration of this dark structureless matter. The central strand is at best faint and is clear in only two thallus branches. The rest show no central strand at all. The oblique ribs though not always seen are more widespread. I think that the pattern of cell-like polygons represents true cells and is not some effect of poor preservation, for instance the imprint of sand grains on a thin coaly layer. At best they certainly look like cells and associated with *T. valdensis* are small fragments of equally delicate plant tissue, also one layer thick but with quite differently shaped cells. One of these fragments is the small leaf described here as ?Bryophyte leaf; another is more like a fern ramentum with very narrow cells. In neither is there any possibility that the cellular pattern has been imposed by sand grains.

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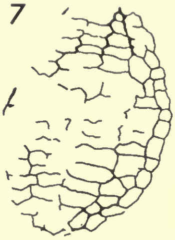

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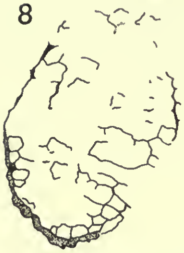

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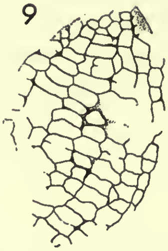

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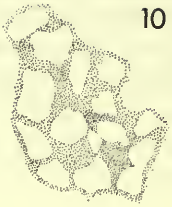

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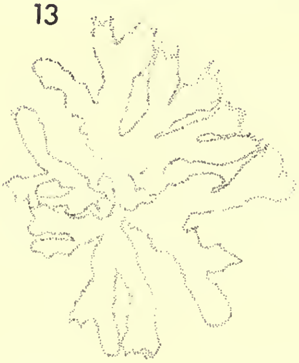

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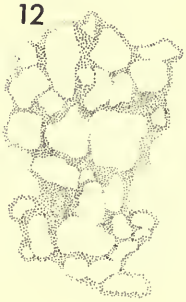

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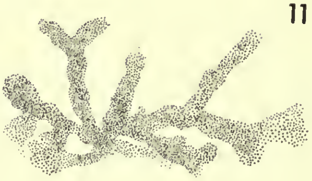

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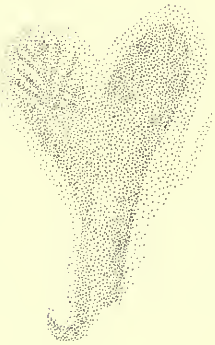

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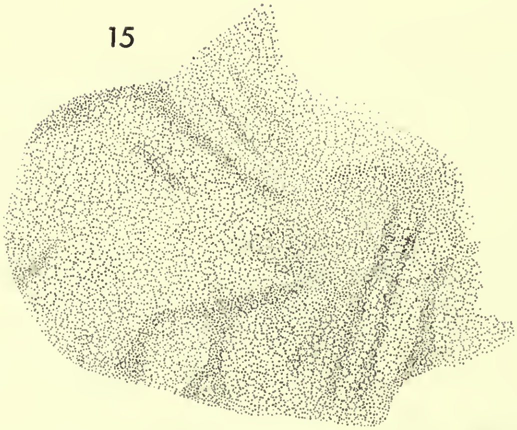


Figs. 7–9. (?) Bryophyte leaf. 7, 8, 9. Leaf showing a single layer of cells. Figs. 8, 9 are part and counterpart. Fig. 7, V.2857*b*. Figs. 8, 9, V.2857. All × 20.

Figs, 10, 11. *Thallites catenelloides* (Seward). 10. Part of specimen showing cells. V.2857. × 100. 11. Part of thallus. V.2857. × 4.

Figs. 12–15. *Thallites valdensis* (Seward). 12. Part of specimen showing cells. V.2857. × 100. 13. Rosette shaped thallus suggesting preservation *in situ*. V.2857*b*. × 1. 14. A branch of the thallus showing thinner peripheral region and ribs of the thicker central region. V.2857*b* × 4. 15. Apex of branch showing the pattern of divergent ribs. V.2857*b*. × 15.

No Marchantialean air chambers are visible, nor is there any clear suggestion of two superimposed layers of cells, though presumably further layers do occur, at least on the midrib and lateral ribs. No rhizoids are present.

Transfers were made but these yielded no additional information. *Chondrus crispus*, the red alga with which Seward compared T. *valdensis* was found to be quite unlike it in having a much thicker thallus and cells of very different shape.

COMPARISON. *T. catenelloides* has a thallus of similar texture but is a much smaller plant. Of the other British Wealden forms *Hepaticites zeilleri* differs in its clearly marked midrib and strong rhizoids. *H. ruffordi* differs in its strong pattern of arcuate ribs.

Most thalloid liverwort-like plants have a broad and strongly marked midrib. The following which are of similar dimensions to *T. valdensis* have only a faint midrib.

T. uralensis Kryshtofovich & Prynada (1933) from the Rhaeto-Liassic of U.S.S.R. is rather narrower and has more pointed lobes. No microscopic details are known.

Hepaticites rosenkrantzi Harris (1931, 1937) from the Lower Lias of East Greenland has no midrib but is two cells thick, the cells tending to be elongated and in rows.

H. amauros Harris (1937), also from the Lower Lias of East Greenland, has a midrib which is a dark, narrow strip but the thallus is many cells thick.

Thallites catenelloides (Seward) comb. nov.

Text-figs. 10, 11

1894 *Algites catenelloides* Seward : 7, pl. 1, figs. 1, 2.

EMENDED DIAGNOSIS. Plant thalloid; thallus dichotomously branched, branches about 0·5 mm. wide; margins probably entire. Thallus composed of uniform tissue one cell thick; cells thin walled, diameter about 50 μ.

HOLOTYPE. V.2857.

DESCRIPTION. Numerous specimens occur on the same blocks as *T. valdensis* and in some cases they are closely associated. The specimens of *T. catenelloides* vary from small fragments to what are probably whole thalli measuring 1 cm. across. They do not form rosettes. The narrow ribbon-like thallus branches frequently and in parts appears to have an undulating though entire margin. The specimen in Text-fig. 11 is the same as that figured by Seward. His suggestion that the thallus has constrictions similar to the red alga *Catenella* seems to be based only on the appearance of part of this particular thallus. It is not seen in the other specimens and is probably due to the undulating margin.

The cells of the thallus are identical with those of *T. valdensis* and the description for that species will serve for both. Transfers were made but these showed only the single layer of cells composing the thallus.

COMPARISON. In *Catenella opuntia* the thallus is several cells thick and has a surface layer of cells much smaller than those of *T. catenelloides*, whilst the central cells are larger and elongated.

All other Mesozoic hepatics, including the three other English Wealden species, are much larger than *T. catenelloides*. The only plants of similar dimensions are from the Carboniferous. Two rather similar fossils are *Thallites willsi* Walton (1925, 1928, 1949) and *Hepaticites langi* Walton (1928). Neither has a definite midrib, both differ in being more than one cell thick and *H. langi* has well marked rhizoids. *T. willsi* which is more comparable has a rather broader thallus.

PTERIDOPHYTA

LYCOPODIALES

SELAGINELLACEAE

Genus ***SELAGINELLA*** Spring

Only one other *Selaginella* from the Mesozoic, *S. hallei* Lundblad (1950*a*), is known in as much detail as the Wealden species described below and referred here to the living genus.

The genus *Selaginellites* Zeiller (1906) was originally used for heterosporous fossils having more than four megaspores in each megasporangium and was thought to differ in this respect from the Recent genus *Selaginella*. Subsequently it was used by Halle (1907) for all heterosporous fossils regardless of the number of megaspores. Later work proved that living species may produce more than four megaspores in each megasporangium (Duerden 1929). Miner (1932) used *Selaginellites* for isolated megaspores which would ordinarily have been called *Triletes* but Harris (1935) recommended that its use should be restricted to fossil shoots which showed evidence of being closer to *Selaginella* than any other genus. Dijkstra (1949) was the first to place the English Wealden species in *Selaginella* but this may have been inadvertent as he later returned to the use of *Selaginellites* without comment. I consider that the Wealden species in no way differs from a typical anisophyllous *Selaginella* with the normal number of four megaspores in each megasporangium and it has, therefore, been referred to the living genus.

Selaginella dawsoni (Seward)

Text-figs. 16–24

1894 *Plantae incertae sedis* Seward : 20, pl. 1, figs. 8, 9.
1913 *Selaginellites Dawsoni* Seward : 87, text-fig. 1.
1913*a* *Selaginellites Dawsoni* Seward; Seward : 86, pl. 4, figs. 1–7.
1949 *Selaginella Dawsoni* (Seward) Dijkstra : 19. (name in list).

DIAGNOSIS. Fertile, dichotomously branched shoots; sterile portion of shoot in part known about 1 mm. wide, dorsiventral, covered with small overlapping leaves. Leaves anisophyllous, in four ranks; leaves of upper two rows alternating and appressed to stem; rhomboid in shape, about 0·5 mm. long; leaves of lower two rows longer, probably about 1 mm. long, slightly spreading laterally but pointing towards apex. Strobilus terminal, unbranched, 2 mm. wide, at least 3 cm. long. Overlapping sporophylls decussately arranged, apparently all alike and longer than leaves, about 1·5 mm. Sporangia more or less rhomboid in outline about 0·5 mm.

across. Megasporangia fewer but distributed throughout length of strobilus; each containing four megaspores. Megaspore with rounded dorsal surface, ventral surface formed by three flattened contact facets; diameter 285 μ–340 μ (mean 306 μ); height about 15 % less; tri-radiate ridges very broad, about 30 μ high, edge rounded, not divided; length equal to radius of spore; arcuate ridges absent. Ventral surface crowded with tubercles, circular or oblong and 5–12 μ across; tubercles also present on surface of tri-radiate ridges but less prominent. Dorsal surface of spore having a coarser pattern of widely spaced ribs, irregular in shape, about 4 μ wide and up to 60 μ long; spore surface smooth between ribs. Spore wall easily separable into two distinct layers, outer 20–30 μ thick, inner about 2 μ thick. Inner membrane straw-coloured and indistinctly marked with small pits. Substance of wall, including tubercles and ribs, light brown in colour and composed of minute granules.

Microsporangia contain numerous microspores which are almost spherical but with flattened contact facets; average diameter 45 μ (range 38-52 μ); tri-radiate mark fine but distinct, equal to about two thirds of spore radius. Contact facets seen as three lobes separated by tri-radiate marks not quite reaching notches between lobes; surface of facets more or less covered with indistinct tubercles, 1–2 μ in diameter. Spore wall distinctly two layered, together only about 2 μ thick at facets but 5–6 μ thick elsewhere. Outside facets both layers uneven in thickness; inner layer becoming thicker opposite a thin place in the outer. Maximum thickness of inner layer about 3 μ, outer about 5 μ.

HOLOTYPE. V.2328.

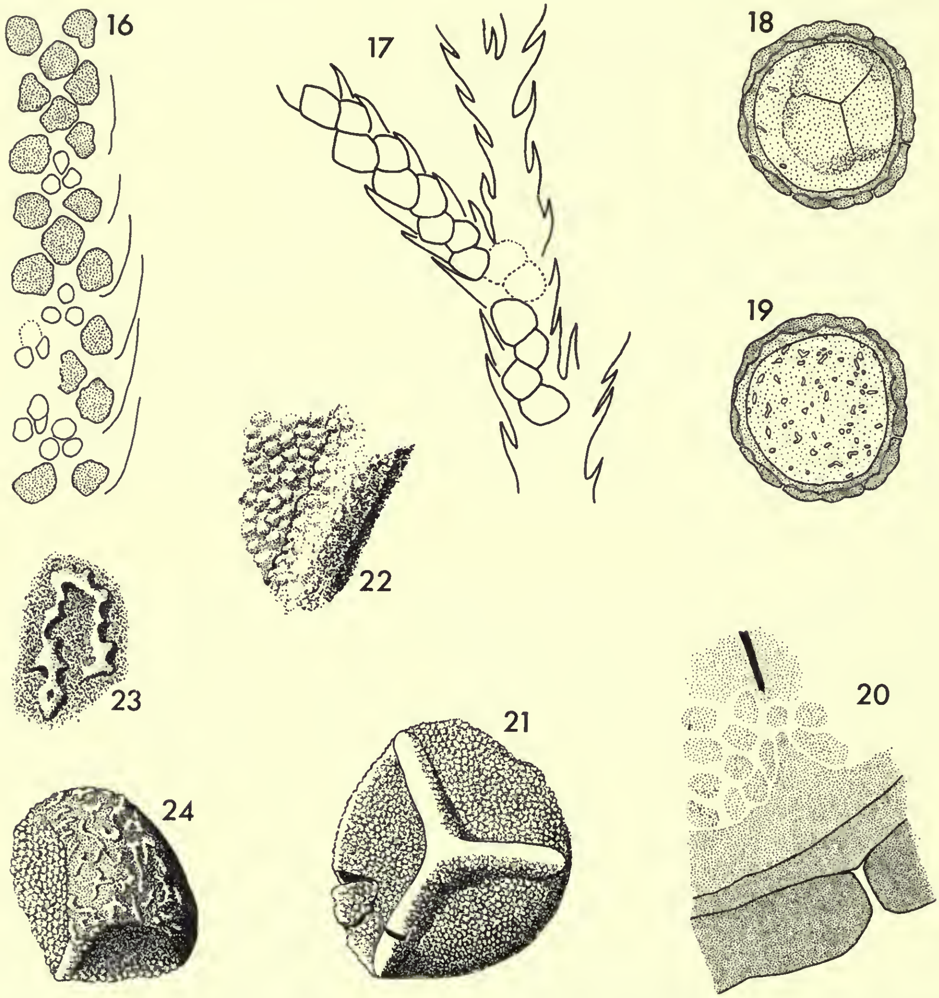
DESCRIPTION. The only material available consists of two fragments of shoot and a few lengths of cone which are present on two blocks of ironstone. Some of the cone specimens have been much damaged. The two shoots are each about 3 cm. long and frequently branch dichotomously. For the most part the sterile portion of the plant is seen merely as a faint outline on the rock, the stem and some of the leaves being replaced by a white mineral and scarcely any carbonaceous plant material remains. On only one or two branches can the phyllotaxis be worked out. Here the mineralized outlines of the dorsal leaves are seen in surface view and the ventral leaves in side view. This is the portion of shoot seen in Text-fig. 17. Although the margins of the leaves are shown as entire it is impossible to tell whether they are correctly represented since the precise margins are unrecognizable. All that is known of the shape of the ventral leaves is from what they show in side view. They are seen to have thicker tissue in the centre. The exact arrangement of the dorsal leaves just behind a dichotomy is uncertain.

The most complete strobilus is 3 cm. long but is probably incomplete, ending as it does, very sharply at the edge of the rock. Although this strobilus does not have any attached sterile part, each of the two shoots have bases of similar strobili attached to one of their branches. Three portions of cones lying close to one another and parallel indicate that a number of them were borne terminally on the plant.

The sporangial walls are not preserved though the outlines of the microspore masses are clearly seen. Only one tetrad of megaspores is present in the megasporangium.

The sporophylls are seen only at the periphery of the strobilus in side view, their general shape being unknown.

Slides of detached spores prepared by Dr. W. Chaloner and kindly lent by him show in most of the megaspores the two very distinctive ornamentations of the



Figs. 16–24. *Selaginella dawsoni* (Seward). 16. Part of a strobilus with microsporangia, megaspores in outline and sporophylls in side view. V.3151. × 10. 17. Part of a sterile shoot showing anisophylly. Holotype, V.2328. × 10. 18. Ventral surface of microspore showing contact facets, tri-radiate marks and two-layered wall in optical section. V.3151*e*. × 500. 19. Dorsal surface of the same spore. V.3151*e*. × 500. 20. Detail from the same spore showing tubercles on contact facets. V.3151*e*. × 2500. 21. Ventral face of megaspore. Specimen lost. × 100. 22. Detail of megaspore showing broad tri-radiate ridge and facet with tubercles. V.3151*y*. × 250. 23. Single rib from dorsal surface of megaspore. V.3151*y*. × 250. 24. Megaspore in side view showing dorsal surface, two facets and a tri-radiate ridge. V.3151*y*. × 100.

different surfaces and a number of broken specimens show the two separate layers of the spore wall. The thin inner layer is easily removed and mounted in glycerine jelly without further treatment. Very brief maceration of the the thick outer coat renders it transparent before mounting. Some of the megaspores do not show the two distinctive sculptures quite so clearly as the figured specimens. In these the dorsal ribs are not so coarse and well defined. Lack of abundant material prevents more detailed study of this variation.

Some of the mounted microspores remain in tetrads but most of them occur singly. The layers of the wall are clearly seen in optical section, their irregular adjacent surfaces closely interlocking, the one being at its thickest where the other is thinnest. The pits in the outer wall while most numerous on the dorsal side also occur on the ventral side but not on the facets.

By squashing the spores the thin walled facets may be detached and their surface more easily studied. In some specimens the tuberculate pattern covers the whole surface of the facet but is only marginal in others.

COMPARISON. Only one other Mesozoic *Selaginella* shoot with cone has been described, namely *S. hallei* Lundblad (1950*a*) from the Rhaetic of Sweden. The sterile shoot is similar in size but with slightly larger and more spreading leaves. Like *S. dawsoni* it is anisophyllous, but the leaves are known in more detail. The strobilus of *S. hallei* is much shorter and has sporophylls which are described as spirally arranged but may equally well be described as in alternating whorls of about four. There are four megaspores in each megasporangium. *Selaginellites polaris* Lundblad (1948) is a Selaginelloid cone from the Trias of Greenland. It is much stouter than *S. dawsoni* (7 mm. wide) and has numerous megaspores in each megasporangium.

Selaginella dichotoma Velenovsky (1931) is a sterile shoot from the Cretaceous of Bohemia with more spreading leaves.

Selaginellites nosikovii Kryshtofovich & Prynada (1932) is a sterile shoot from the Jurassic of Siberia which also has larger, more spreading leaves than *S. dawsoni*.

Among living species *S. sanguinolenta* is very similar in size and leaf arrangement, but the spores are different the megaspores being of similar size but with much more prominent tubercles on the dorsal surface.

S. emmeliana possesses strikingly similar megaspores to those of *S. dawsoni* with the same shape and sculpturing both on the dorsal and ventral surfaces. *S. emmeliana*, however, possesses other megaspores which show a great deal of variation both in size and surface ornament. Not all have different dorsal and ventral patterns, some having the coarse ribbed pattern on both surfaces whilst others have the fine tuberculate pattern on both. The foliage of *S. emmeliana* is quite different from that of *S. dawsoni*.

EQUISETALES

Genus *EQUISETITES* Sternberg

REMARKS. The external morphology of *E. lyelli* has been fully described by Allen (1941). Additional information about this species (Watson 1964) was obtained from some petrified fragments found by Mr. P. Whybrow (British Museum, Natural History). Very recently Mr. Whybrow has found much more extensive petrified material and in addition new compression material is available with easily prepared cuticle. It will, therefore, be necessary to make a complete revision of the species using all available material, including that described by Allen (1941).

Descriptions of all three species of Wealden *Equisetites* (Seward 1894) will be included in a later volume.

FILICALES

Family *MATONIACEAE*

Genus *MATONIDIUM* Schenk 1871 : 219

Matonidium goepperti (Ettingshausen)

1852 *Alethopteris goepperti* Ettingshausen : 8, pl. 7, fig. 7.
1894 *Matonidium Göpperti* (Ett.); Seward : 63, text-figs. 7, 8.
1913 *Matonidium goepperti* (Ett.); Seward : 89, text-fig. 2C, pl. 14, fig. 3a.
1961 *Matonidium goepperti* (Ett.); Harris : 112, text-figs. 37, 38. (see also for earlier references).

Matonidium goepperti (Ett.) has been fully revised by Harris (1961) using abundant, well preserved material from the Yorkshire Jurassic. The English Wealden material is scanty and ill-preserved but agrees in all available characters with the Yorkshire material and I regard the two as specifically identical.

Family **DIPTERIDACEAE**

Genus *HAUSMANNIA* Dunker 1846 : 12

Hausmannia dichotoma Dunker

Pl. 3, figs. 1, 2

1846 *Hausmannia dichotoma* Dunker : 12, pl. 5, fig. 1; pl. 6, fig. 12.
1894 *Dictyophyllum Roemeri* Schenk; Seward : 140, text-figs. 16, 17.
1906 *Hausmannia dichotoma* Dunker; Richter : 18, pls. 3–6.
1913 *Hausmannia pelletieri* Seward : 89, pl. 14, figs. 1–3.
1961 *Hausmannia dichotoma* Dunker; Harris : 126, text-fig. 43.

This species is widespread in the Lower Cretaceous of Europe and less common in the Jurassic. It has been revised by Harris (1961) who gives an emended diagnosis based on Richter's material (Lower Cretaceous; Germany) and on Yorkshire Jurassic specimens. The leaves of *H. dichotoma*, both sterile and fertile, are quite well known but nothing is yet known of the sorus. The English Wealden material consists of a few imperfect sterile leaves which add nothing to our knowledge of the species. The best examples are figured in Pl. 3, figs. 1, 2.

Family **SCHIZAEACEAE**

Genus ***RUFFORDIA*** Seward 1894 : 75

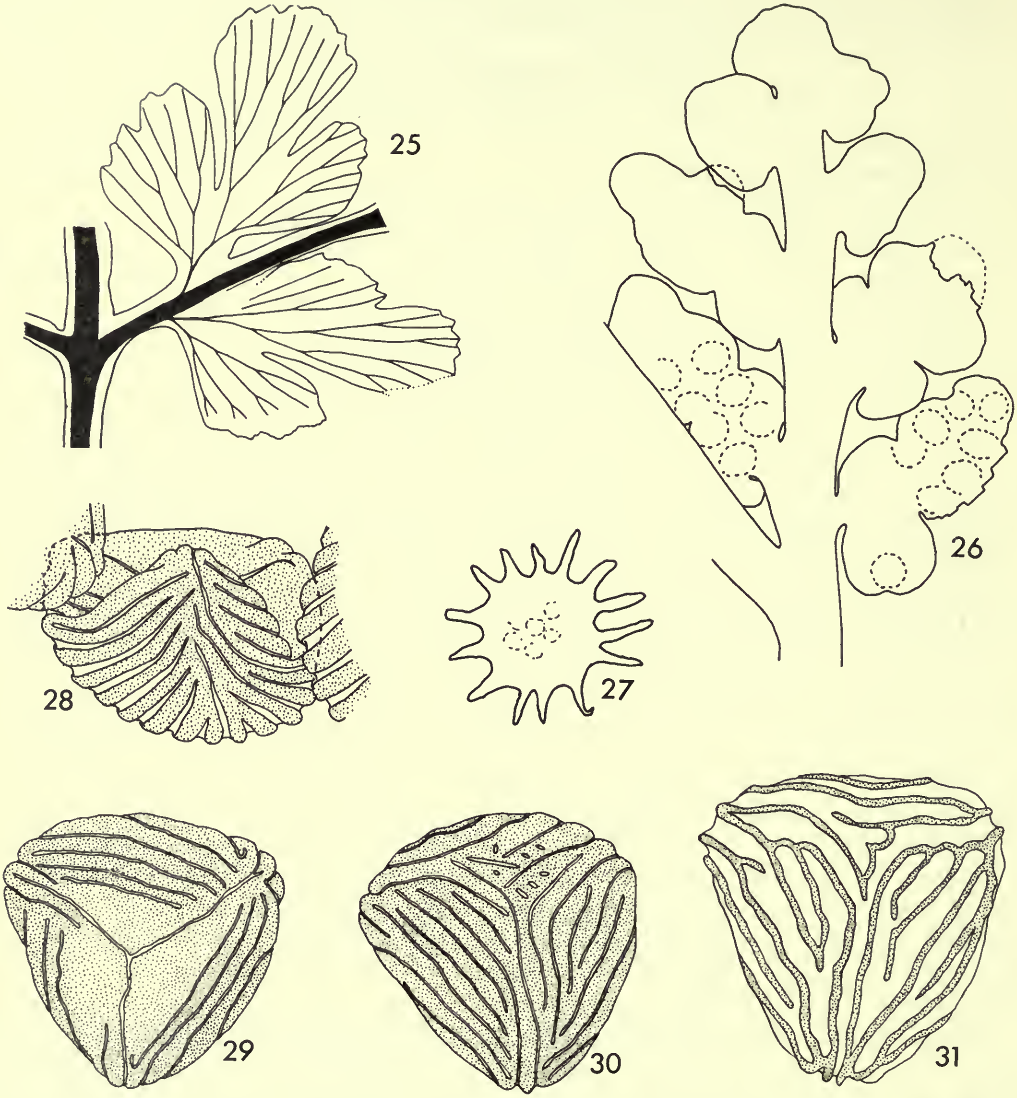
Ruffordia goepperti (Dunker)

Pl. 4, figs. 1–7; Pl. 5, figs. 1–4; Text-figs. 25–31.

Selected references:
1843 *Cheilanthites Göpperti* Dunker : 6.
1894 *Ruffordia Göpperti* (Dunker) Seward : 76, pl. 3, figs. 5, 6; pl. 4; pl. 5, figs. 1–5.
1894 *Ruffordia Göpperti* (Dunker) var. *latifolia* Seward : 85, pl. 6, figs. 1, 1*a*.
1910 *Ruffordia Goepperti* (Dunker); Seward : 350, text-fig. 260 A–C. (figures repeated from Seward 1894).
1913 *Ruffordia goepperti* (Dunker); Seward : 91, text-fig. 2A. (drawing of a spore).
1921 *Ruffordia Goepperti* (Dunker); Halle : 10, pl. 2, figs. 1–8.
1958 *Ruffordia goepperti* (Dunker); Couper : 109, pl. 17, figs. 4–6. (photographs of spores).
1966 *Ruffordia goepperti* (Dunker); Hughes & Moody-Stuart : 274, pl. 43, figs. 1–12. (spores).

EMENDED DIAGNOSIS. Frond triangular, tripinnate to quadripinnate; rachis slender. Pinnae triangular or ovate; primary pinnae nearly opposite; secondary pinnae increasingly alternate. Sterile and fertile parts distinct. Sterile pinnules variable in width, decurrent; narrow pinnules linear, apices mucronate or acute, venation Coenopterid; wider pinnules ovate, Sphenopterid, with small marginal tooth at each vein ending. Fertile pinnules reduced in length but not breadth; more widely outspread, not decurrent, margins undulating, apices bluntly rounded. Sporangia borne singly on underside of pinnules without indusium; typically twelve on a pinnule, arranged in two longitudinal rows. Annulus transverse, apical,composed of about fifteen to twenty-five long narrow cells radiating from a central plate; extending at least to middle of sporangium. (Remaining parts of sporangium unknown, spore number uncertain). Spores rounded-triangular with convex sides, typically 45 μ equatorial diameter (range 35 μ to 60 μ), tri-radiate cracks almost reaching corners. Apical parts of facets smooth, rest of facets and whole of distal surface covered with ribs separated by grooves. Ribs forming three sets, each set starting on contact face and extending on to distal surface; in each set ridges nearly parallel. Ridges of a set joining near tri-radiate cracks and also joining, though less regularly, along continuation of tri-radiate cracks onto back of spore. Smooth apical parts of facets as thick as ribs.

DESCRIPTION AND DISCUSSION. *Ruffordia goepperti* (Dunker) is represented by a large number of sterile specimens which show a wide range in the form of the pinnules, the extremes of which are shown in Pl. 4, figs. 1, 4. The specimens with broadest pinnules were designated *R. goepperti var. latifolia* (Seward 1894) but all are now included in *R. goepperti* (Dunker) as there seems to be intergradation, though the possibility of the widest forms belonging to a different species is not excluded. There are three fertile specimens amongst the English material (V.2160 V.2295, V.2192). Two are completely fertile (V.2160 and V.2192) whilst the other (V.2295) has basal fertile pinnae and a sterile top (Pl. 5, fig. 1). Specimens V.2192 and V.2295 are preserved in the characteristic red ironstone and only the spore masses, and sometimes the sporangium annulus, are well preserved, the rest of the



FIGS. 25–31. *Ruffordia goepperti* (Dunker). 25. Broad form of pinnules showing venation. V.2357. × 8. 26. Fertile pinnules showing undulating margins. Broken lines indicate positions of sporangia. V.2160. × 15. 27. Sporangium showing thickened walls of annulus. V.2295. × 100. 28. Spore in equatorial view showing widely spaced ribs and shapes of ribs in section, i.e. rounded, flattened, grooved. Slide from V.2160, × 750. 29, 30. Proximal and distal surfaces of the same spore showing wide ribs closely spaced. Slide from V.2160, × 750. 31. Spore with narrow ribs and wide grooves. Slide from V.2192*b*, × 750.

frond being only a faint impression on the rock. This is a typical condition of the plants in this matrix but it is sometimes useful for details of venation (Pl. 4, fig. 7). Specimen V.2160 in a soft, fine, grey siltstone matrix is much better preserved though the frond is heavily varnished and badly cracked. Text-figure 26 shows the rounded lines of the fertile pinnules with a lobed appearance. The specimen presents the upper surface of the frond and the sporangia below are seen only in faint outline. A balsam transfer revealed no details of the sporangia.

The spores of *R. goepperti* (Dunker) were inadequately figured by Seward (1913, text-fig. 2A) using V.2192 and by Couper (1958, pl. 17, figs. 4–6) using Seward's slide preparation. Recently the spores have been studied in detail by Hughes & Moody-Stuart (1966) using V.2192 and Seward's slide mentioned above. I have found that V.2192 yields spores which are somewhat different from those of V.2295 and V.2160. The spores agree in size range and general form but differ in details of sculpturing. The spores from V.2295 and V.2160 have ribs (muri) from 2 μ to 5 μ wide separated by furrows (lumina) 0·5 μ to 2 μ wide but the ribs of any particular spore are always wider than the furrows and the majority of spores have ribs about 3 μ wide and furrows 1 μ wide (Text-figs. 28–30). The ribs vary in profile and may be rounded, flattened or indented; this variation is seen in Text-fig. 28. Spores from V.2192 have the sculpture in almost exactly the reverse proportions (Text-fig. 31), the ribs being 1 μ to 2 μ wide and spaced 2 μ to 5 μ apart. Hughes & Moody-Stuart (1966) give a detailed diagnosis of these spores and numerous figures. I have prepared spores from various parts of V.2192 but I have been unable to find any with broad ribs. Neither V.2295 nor V.2160 yielded spores with narrow ribs and I could find no suggestion of gradation between the two types of spores.

The identity of V.2192 is not in doubt, however, because in all other respects it agrees perfectly with the other two specimens. It is closely similar to the basal pinnae of V.2295 and also has undulating pinnules as in V.2160.

Fertile specimens of *R. goepperti* (Dunker) from Manchuria were figured by Halle (1921) including photographs of the sporangia, each represented by a well preserved annulus. This annulus is certainly an apical ring of the Schizaeaceous type. Halle's photographs show the long annulus cells radiating from a small circular space or " plate ". This suggests that the annulus cells in Text-fig. 27 do not show their full length, although he does report cases where the " central area seems to be much wider than others ". Halle removed what he considered to be a whole sporangium and gives three countings in the region of 400. I have removed what appeared to be whole sporangia from the balsam transfers and obtained various counts under 100. I regard my counts as highly suspect as it was difficult to be sure that the spore masses were whole sporangia. One cannot know how reliable Halle's count is but he reports that " in some cases it was possible to remove the whole contents of a sporangium more or less intact ". In living members of the Schizaeaceae the spore output is 128 or 256. Hughes & Moody-Stuart (1966) regard the spores of Halle's material as of a different type from those found in *R. goepperti* (Dunker) from the English Wealden. However, his photographs of sterile and fertile fronds appear to be very similar to the English specimens. One of them (pl. 2, fig. 2) shows short, undulating, fertile pinnules. Halle's photograph of the spores (pl. 2, fig. 8) is a poor one and considering the spore differences in the English specimens of *R. goepperti* (Dunker) I have retained the Manchurian material within the species until it can be proved otherwise. Certain details of the sporangium in the diagnosis above are based on Halle's account.

Among living genera of the Schizaeaceae, *R. goepperti* (Dunker) most resembles *Anemia* with its distinct and reduced fertile pinnae. The sterile frond of *Anemia adiantifolia* is very similar in form to the broader specimens of *R. goepperti* whilst the narrow pinnules closely resemble *Anemia cuneata* (Bower 1926, text-fig. 440).

The sculptured spores of the genus *Mohria* are of exactly the same type as *R. goepperti* (Dunker). This type of spore also occurs in the other Wealden Schizaeaceous fern, *Pelletieria valdensis* Seward and a comparison is included in the descrition of that species.

Genus ***PELLETIERIA*** Seward 1913 : 91

Pelletieria valdensis Seward

Pl. 6, figs. 1, 2; Text-figs. 32–40

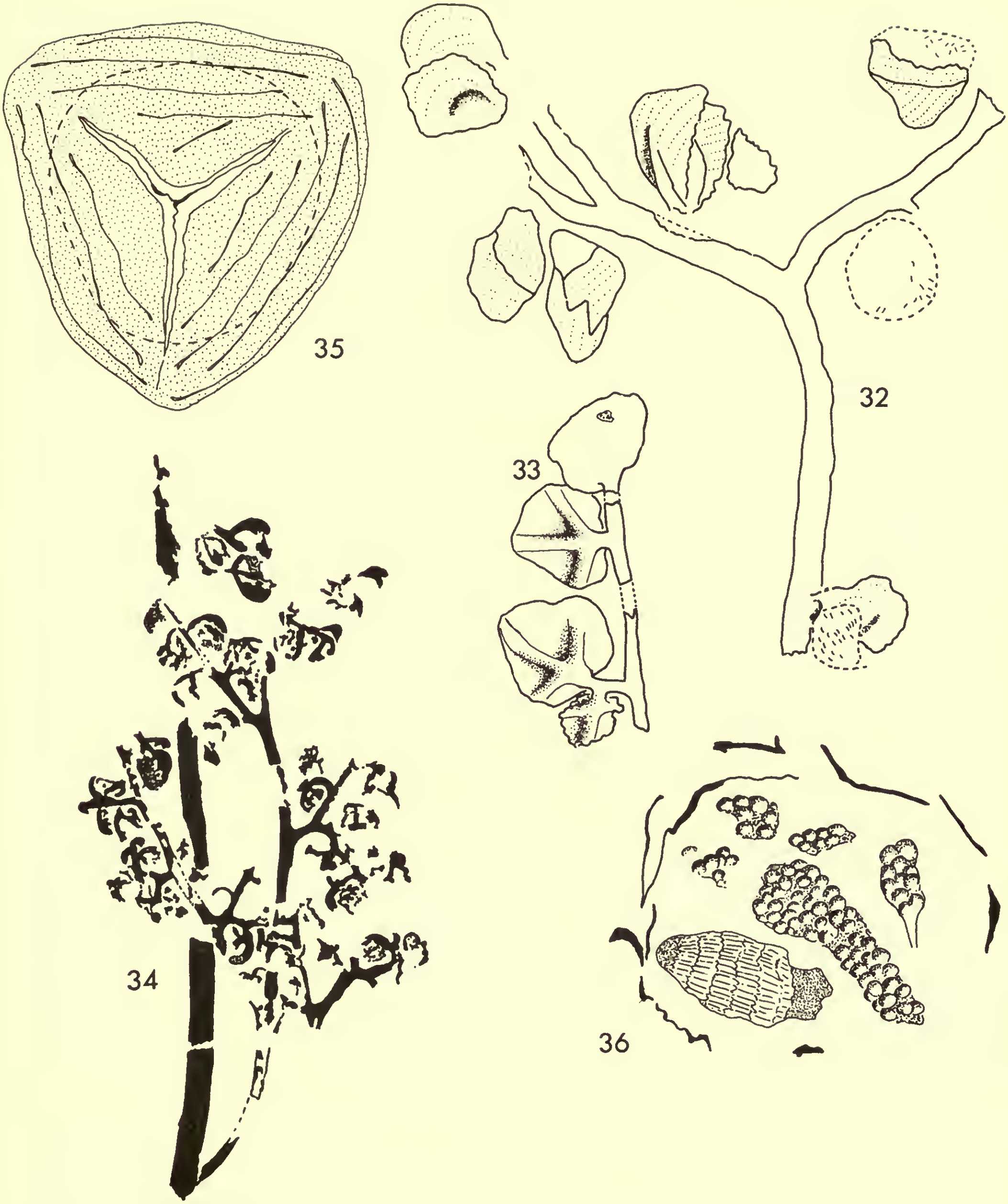
1913 *Pelletieria valdensis* Seward : 91, text-figs. 2B, 3, 4; pl. 12, figs. 12*a*, 12*b*; pl. 14, fig. 5.
1958 *Pelletieria valdensis* Seward; Couper : 109.
1966 *Pelletieria valdensis* Seward; Hughes & Moody-Stuart, pl. 44, figs. 1–8; pl. 45, figs. 1–7.

EMENDED DIAGNOSIS. Known only from fertile specimens. Frond at least quadripinnate; consisting of slender axis branched repeatedly, with no lamina except at tips of ultimate branches. Tips bearing groups of fertile pinnules; each pinnule tightly rolled, completely enclosing the sporangia. Each rolled pinnule more or less spherical, 2 mm. across, enclosing at least ten sporangia; sporangium elongated, sessile or shortly stalked, wall composed of small elongated cells, longitudinally orientated. (Annulus unknown). Spores rounded-triangular with tri-radiate cracks of medium length; surface sculptured with a pattern of flat ribs 3–7 μ wide separated by narrow grooves 0·5–2 μ wide.

LECTOTYPE. V.2329. Selected Hughes & Moody-Stuart 1966.

DESCRIPTION. *P. valdensis* Seward is represented by several specimens all of which are fertile. Fragments of pinnae and detached fertile " capsules " are abundant but there are only two assembled groups of pinnae, specimens V.2368 and V.2329. Both of these syntypes were figured by Seward (1913, text-figs. 3B, B′; pl. 12, figs. 12*a*, *b*.) and V.2329 (Text-fig. 32) has recently been selected as Lectotype by Hughes & Moody-Stuart (1966). After I picked away the matrix V.2368 is now a better specimen, more extensive and better preserved than V.2329 (Pl. 6, figs. 1, 2, Text-fig. 39).

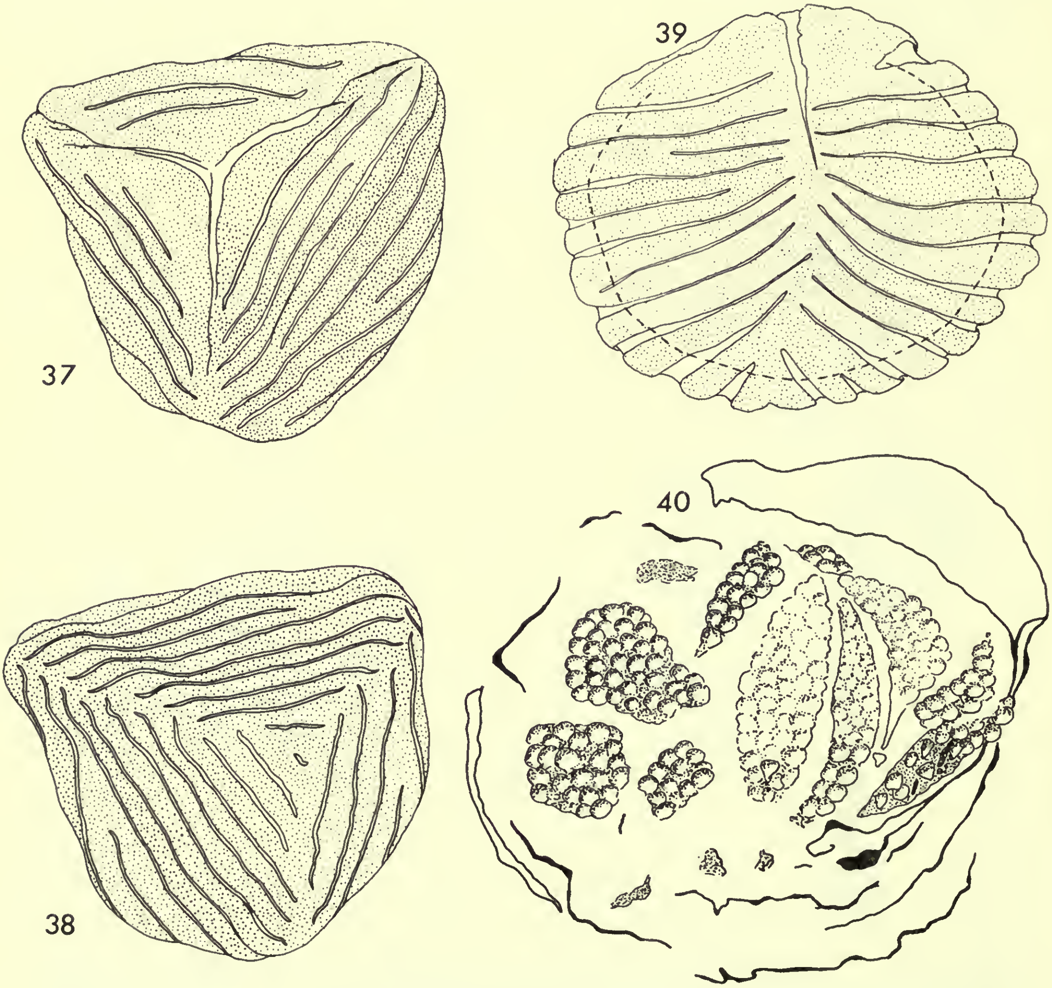
The exact form of the fertile " capsules " is far from fully understood. A number of isolated " capsules " were dissolved out of the rock in HF but revealed nothing more about their structure than is shown in the Lectotype which clearly shows the folded nature of the pinnules (Text-fig. 32). A number of specimens show hairs in the matrix where " capsules " have been removed (Text-fig. 32) but such hairs could



Figs. 32–36. *Pelletieria valdensis* Seward. 32. Lectotype showing folded " capsules ", hairs and cell directions (indicated by dotted lines). V.2329. × 6. 33. Small specimen with three ribs on the " capsules ". V.51846. × 6. 34. Largest assembled shoot showing dissected form of frond. V.2368. × 3. 35. Spore showing thickness of wall (indicated by dotted line) V.51841. × 750. 36. Eroded " capsule " with one sporangium showing cells of the wall. Others showing spores. V.51847. × 35.

not be found on any of the specimens dissolved out. Certain specimens show the axis continued as a rib over the back of the rolled fertile pinnules and this rib is branched in V.51846 (Text-fig. 33). The pinnules of V.51846 appear less tightly rolled than others and might well prove worth sacrificing to a balsam transfer. That this specimen is fertile is not in doubt as spores can be seen through a broken part at the top.

Because the sporangia are completely enclosed they could only be studied in certain eroded " capsules " which show sporangia in various attitudes (Text-fig. 40).



FIGS. 37–40. *Pelletieria valdensis* Seward. 37, 38. Proximal and distal surfaces of the same spore. Slide from V.2329, × 750. 39. Equatorial view of spore showing widely spaced ribs. Slide from V.51841, × 750. 40. Eroded " capsule " with folded pinnules in section and spores in sporangia. V.51840. × 35.

Attempts to isolate a sporangium failed because the plant material crumbles very easily into small fragments: thus the spore number is not known. However, on such a sporangium as in the centre of Text-figure 40 around fifty spores can be counted on the surface but because only one layer can be seen it seems probable that the contents are at least twice this figure. One sporangium seen in surface view (Text-fig. 36) shows the cells of the wall, small, elongated and longitudinally orientated; although there is no indication of the annulus.

The spores of *P. valdensis* Seward have recently been redescribed by Hughes & Moody-Stuart (1966) using Seward's figured slide preparation from V.2329 (1913) and new preparations from V.2329. They found the size range to be 52–98 μ with 80% of specimens between 63 μ and 84 μ maximum diameter. My preparations from V.2329 and V.21841 agree well with these figures but V.2368 yielded somewhat larger spores, 56–115 μ (100 measured) with 75% between 75 μ and 105 μ. Hughes & Moody-Stuart (1966) have diagnosed, described and figured the spores in detail and there is nothing more to add.

COMPARISON. The ribbed spores of *P. valdensis* Seward are typically Schizaeaceous and very similar to those of various living and fossil species. However, the form of the fertile fronds cannot be matched; the living members of the Schizaeaceae merely having curled margins protecting the sporangia. The only comparable structure I know is in the species *Onoclea sensibilis* Linn, where the fertile pinnules are narrow and so tightly inrolled as to completely enclose the sporangia.

The spores of *P. valdensis* are similar in form to those of *Ruffordia goepperti*, particularly the form with the broad ribs and narrow grooves, but they are quite easily distinguishable on size difference alone. The upper limit found for the diameter of *R. goepperti* was 60 μ and the lower limit for *P. valdensis* 63 μ. A most distinct difference is the thickness of the exine; in *R. goepperti* about 4 μ (including the thickness of the ribs) whilst in *P. valdensis* (Text-fig. 35) it varies from about 5 μ to 15 μ. This variation depends upon the spaces between ribs being open or closed and is dealt with in some detail by Hughes & Moody-Stuart (1966 : 280–282). A further difference is that the ribbed pattern in *P. valdensis* extends on to the contact facets whilst in *R. goepperti* the facets are smooth.

Family **POLYPODIACEAE**

Genus ***ASPIDISTES*** Harris, 1964 : 181

The type species of this genus, *Aspidistes thomasi* Harris, is the only other Mesozoic fern I know with the *indusium superum* and other aspidioid characters. Although various diagnostic characters of *Aspidistes* are not known for *Aspidistes sewardi* sp. nov. the form of its indusium and spores give it a good measure of agreement. The slight difference in spore number (*A. thomasi* has forty-eight)is not important. However, further details of the sorus and sporangium may well show it to be generically distinct. Various other genera exist whose names suggest close affinity with *Aspidium* or *Polystichum* but are based only on sterile specimens.

Aspidistes sewardi sp. nov.

Pl. 6, figs. 3, 4; Text-figs. 41–43

1894 *Weichselia mantelli* (Brongniart) Seward : 121.

DIAGNOSIS. (Based on single fertile pinna V.2173*a*). Pinnules arising from upper surface of rachis at an angle of 50–60°; pinnules 2 mm. long, 1·5 mm. broad, apex rounded; joined to each other at base by a narrow web; margin of pinnules and web rolled. Groups of three sori borne on under surface of each pinnule; two larger adjacent to the rachis. Each sorus with a thick peltate indusium covering about twelve sporangia arranged in a circle. Sporangium containing thirty-two spores (sporangial wall unknown). Spores trilete, smooth walled, thickened at corners; narrow bands of thickening flanking triradiate crack. Arms of triradiate crack nearly reaching corners, sometimes bifid at ends; diameter 60–75 μ.

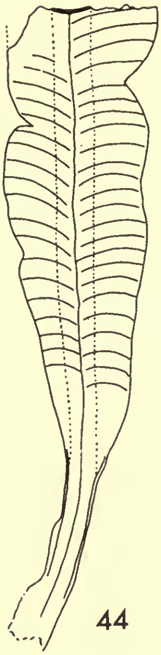
HOLOTYPE. V.2173*a*, the only specimen.

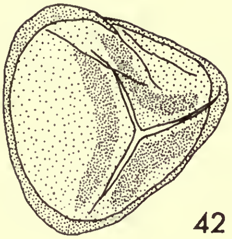
DESCRIPTION. The single specimen (V.2173*a*) is 6·5 cm. long and was formerly referred to *Weichselia mantelli* (= *W. reticulata* Stokes & Webb) by Seward (1894) its form being very similar to the smaller pinnules of that species. However its abaxial surface is uppermost and on moistening with paraffin the sori are clearly visible to the naked eye (Pl. 6, fig. 4). It is certainly not *Weichselia reticulata* for fertile material of that species is included in the Bommer Collection and it is quite different (correspondence with Dr. K. L. Alvin).

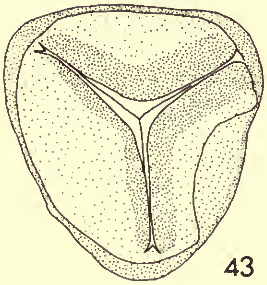
Unfortunately the specimen is heavily impregnated with glue and the substance of the fossil is badly crumbling, making it very difficult to examine the details of the sorus. The water soluble gum swells rather violently when wet and lifts the fossil fragments off the surface of the rock. Careful picking with a fine needle revealed a certain amount of information. The circular indusium appears to be quite thick and is probably attached by a central stalk; details of its cellular structure could not be seen. The sporangia are distinct pear-shaped masses, about twelve in number, in a ring under the indusium and sometimes a few under the rolled margin of the pinnule. They were easily removed intact to count the spores. Of the twelve sporangia macerated and counted nine contained thirty-two spores and three others contained twenty-nine, thirty, and thirty-one. The sporangial wall was not seen either in the untreated sporangium or during maceration.

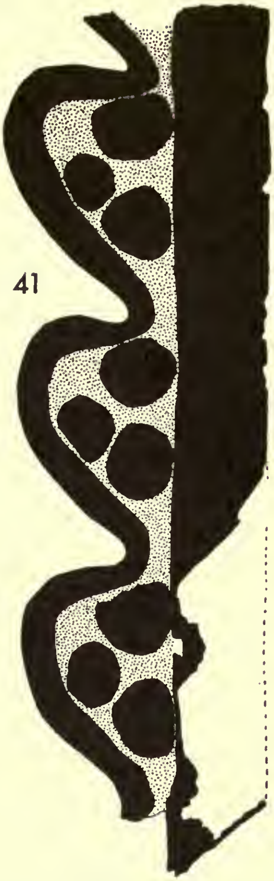
Among the Wealden ferns there are few species of sterile fronds to which this specimen could belong but it is similar to one described as *Dichopteris delicatula* Seward (1913 pl. 11, figs. 6*a*, *b*). Possibly further specimens, sterile or fertile, are among the *Weichselia reticulata* material but nothing is known of its venation and it is not always clear in *Weichselia*. Furthermore any specimen with the adaxial side upwards would easily be missed.

COMPARISON. Amongst living genera *A. sewardi* is most similar to *Polystichum* agreeing in the form of the indusium and the spore output. However all living species of the Aspidieae have wedge-shaped spores whereas both *A. sewardi* and *A. thomasi* Harris have trilete spores.









FIGS. 41–43. *Aspidistes sewardi* sp. nov. 41. Three pinnules showing shape, rolled margins and sori. V.2173*a*, × 15. 42, 43. Two spores. Triradiate crack in Fig. 43 with bifid ends. Fig. 42, slide ii from V.2173*a*, × 750. Fig. 43, slide i from V.2173*a*, × 500.
FIG. 44. *Nilssonia schaumburgensis* Dunker. Base of leaf. Specimen L.5532 Manchester Museum, × 5.

A. sewardi is named after Sir Albert Charles Seward who first described the English Wealden flora.

UNCLASSIFIED FERNS

The following are ferns, described by Seward (1894), to which I can add little or nothing.

Cladophlebis longipennis Seward

1894 *Cladophlebis longipennis* Seward : 89, pl. 9, figs. 1, 1*a*.

Cladophlebis albertsii (Dunker)

1894 *Cladophlebis Albertsii* (Dunker) Seward : 91, text-fig. 9; pl. 8.

Cladophlebis browniana (Dunker)

1894 *Cladophlebis Browniana* (Dunker) Seward : 99, pl. 7, fig. 4.
1913 *Cladophlebis Browniana* (Dunker) Seward : 95, pl. 8, figs. 1, 2.

Cladophlebis dunkeri (Schimper)

1894 *Cladophlebis Dunkeri* (Schimper) Seward : 100, pl. 7, fig. 3.
1950 *Cladophlebis* (*Klukia*) *dunkeri* (Schimper); Radforth & Woods : 780, pl. 1.

The various English Wealden specimens, referred by Seward to the four species above, appear to be indistinguishable from each other and *Cladophlebis longipennis* Seward is particularly ill-defined. Indeed Seward himself later wrote (1913) of the " difficulty—or indeed, impossibility—of separating *Cladophlebis browniana* and *Cladophlebis dunkeri* ". Modern treatment of Canadian material referred to *C. dunkeri* (Schimper) by Radforth & Wood (1950) shows the fern to have Schizaeaceous sporangia and spores, though the latter are scarcely distinguishable in the photograph.

Sphenopteris ruffordi (Seward) comb. nov.

1894 *Acrostichopteris Ruffordi* Seward : 61, pl. 6, fig. 3.

Sphenopteris fittoni Seward

1894 *Sphenopteris Fittoni* Seward : 107, pl. 6, fig. 2; pl. 7, fig. 1.

Sphenopteris fontainei Seward

1894 *Sphenopteris Fontainei* Seward : 106, pl. 7, fig. 2.

Leckenbya valdensis (Seward)

1894 *Nathorstia valdensis* Seward : 145, pl. 7, fig. 5; pl. 9, figs. 2, 2*a*.
1894 *Leckenbya valdensis* (Seward) Seward : 384.
1895 *Leckenbya valdensis* (Seward); Seward : 225.
1911 *Gleichenites cycadina* (Schenk); Seward : 664.

Teilhardia valdensis Seward

1913 *Teilhardia valdensis* Seward : 96, pl. 11, figs. 7*a*–9*b*.

Genus ***ONYCHIOPSIS*** Yokoyama 1889 : 26

Onychiopsis psilotoides (Stokes & Webb)

1824 *Hymenopteris psilotoides* Stokes & Webb : 423, pl. 46, fig. 7.
1827 *Hymenopteris psilotoides* Stokes & Webb; Mantell : 55, pl. 1, figs. 3a, 3b; pl. 3, figs. 6, 7; pl. 3*, fig. 2.
1828*a* *Sphenopteris Mantelli* Brongniart : 50.
1828 *Sphenopteris Mantelli* Brongniart; Brongniart : 170, pl. 45, figs. 3–7.
1833 *Sphenopteris Mantelli* Brongniart; Mantell : 241.
1894 *Onychiopsis Mantelli* (Brongniart) Seward : 41, pl. 2, fig. 1; pl. 3, figs. 1–4.
1894 *Onychiopsis elongata* (Geyler); Seward : 55.
1905 *Onychiopsis psilotoides* (Stokes & Webb) Ward : 155, 506, 518, pl. 39, figs. 3–6; pl. 111, fig. 4; pl. 113, fig. 1.

1910 *Onychiopsis Mantelli* (Brongniart); Seward : 378, fig. 280, A, B.
1913 *Onychiopsis mantelli* (Brongniart); Seward : 96.
1961 *Onychiopsis psilotoides* (Stokes & Webb); Tattersall : 349, pl. 12, figs. 1–3.

DISCUSSION. This species was of world wide distribution in the Lower Cretaceous and its remains are known from England, Germany, France, Belgium, Portugal, Russia, Canada, U.S.A., Egypt, South Africa, India and Japan. Although the species has been described numerous times, including fertile parts (Tattersall 1961), it is still imperfectly known. Spores were readily obtained but resemble those of a number of families and do not help in classification. Details of sporangia are still unknown; though some fertile pinnules have a lumpy surface suggestive of sporangia. However the whole surface is covered by an indusium-like sheet of elongated cells and maceration leaves no trace of sporangial walls.

I have been unable to add usefully to our knowledge of this species and consider that the figures of Seward (1894) and Tattersall (1961) cannot be improved upon. In the light of a recent review of this species by Sukh Dev (1965) with an exhaustive synonomy I have given only those references which include the important name changes or refer to the English material.

Genus ***WEICHSELIA*** Stiehler

Weichselia reticulata (Stokes & Webb)

Pl. 6, fig. 5

Selected references:

1824 *Pecopteris reticulata* Stokes & Webb : 423, pl. 46, fig. 5; pl. 47, fig. 3.
1827 *Pecopteris reticulata* Stokes & Webb; Mantell : 56, pl. 3, fig. 5; pl. 3*, fig. 3.
1828*a* *Lonchopteris Mantelli* Brongniart; 60.
1828 *Lonchopteris Mantelli* Brongniart : 369, pl. 131, figs. 9, 10.
1894 *Weichselia Mantelli* (Brongniart) Seward : 114, text-figs. 12, 13.
1899 *Weichselia reticulata* (Stokes & Webb) Ward : 651, pl. 160, figs. 2–4.
1919 *Weichselia reticulata* (Stokes & Webb); Florin : 305, figs. 1, 2–5.
1965*a* *Weichselia reticulata* (Stokes & Webb); Reymanówna : 16, text-fig. 1; pl. 1, figs. 7–11.
1965 *Weichselia reticulata* (Stokes & Webb); Sukh Dev : 73, figs. 7, 8.

DISCUSSION. This widespread Lower Cretaceous species has recently been revised by Reymanówna (1965*a*) and Sukh Dev (1965). Most of the English specimens are mere fragments of pinnae, many of them fusainized, but there is one large, assembled frond in the collection. This is figured by Seward (1894, pl. 10, fig. 3.) and shows the characteristic habit of the plant very well.

The lower epidermis of *W. reticulata* (Stokes & Webb) was first figured by Florin (1919) using Belgian material and Sukh Dev (1965) has figured the epidermis from English Wealden specimens. Reymanówna (1965) gives figures of stomata together with photographs of indusia, but the fertile material of *W. reticulata* (Stokes & Webb) has yet to be fully described. None of the English material is fertile.

Sukh Dev (1965) gives extensive references to older work so that only selected references have been cited above.

SPERMATOPHYTA

PTERIDOSPERMAE

Genus *PACHYPTERIS* Brongniart

1828 *Pachypteris* Brongniart : 49 (Name only).
1829 *Pachypteris* Brongniart : 166.
1964 *Pachypteris* Brongniart; Harris : 121 (Emended diagnosis).

Pachypteris lanceolata Brongniart

Pl. 1, fig. 6; Text-figs. 45–47

1828 *Pachypteris lanceolata* Brongniart : 50 (Name only).
1829 *Pachypteris lanceolata* Brongniart : 167, pl. 45, fig. 1.
1895 *Dichopteris* sp. cf. *D. laevigata* (Phillips) Seward : 184, pl. 12, fig. 6.
1964 *Pachypteris lanceolata* Brongniart; Harris : 137, text-figs. 55–58.

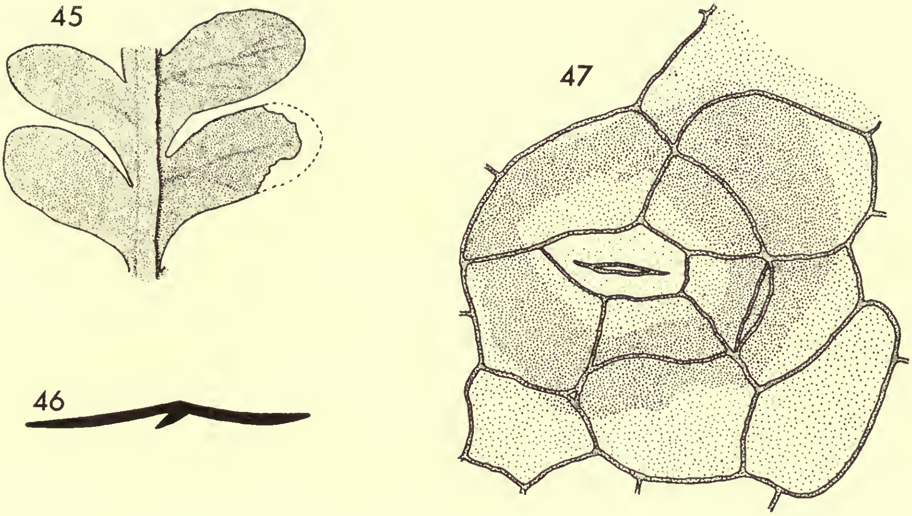
MATERIAL. V. 3245

DESCRIPTION. The following description is based on the only English Wealden specimen known. It is a single pinna, 8 cm. long, 1 cm. wide at the widest part, with two rows of pinnules, leathery in texture. The rachis, up to 700 μ wide, is very prominent on the underside of the pinna. The pinnules arise alternately, usually slightly overlapping but not completely divided and are up to 6 mm. long and 3 mm. wide, narrowing slightly but attached to the rachis by a broad and decurrent base. The pinnules are typically oval and blunt ended. Pinnules at the apex are smaller and less divided; the rachis is not so prominent here. The venation is visible on the lower side of some pinnules projecting slightly above the surface, but concealed in most, the veins consisting of a midrib with a few laterals given off at a fairly low angle. The midrib is broad and situated above the middle of the pinnule where it joins the rachis. The margins of the pinnules are not thickened.

The upper epidermis lacks stomata and has a thick cuticle showing isodiametric cells with smooth walls and without pits. These cells are irregularly arranged except at the margin where they are elongated and tend to be in longitudinal rows, the cells here having thicker anticlinal walls. The lower cuticle is thinner, the cells of the lower epidermis being thin walled, isodiametric and irregularly arranged, except at the margin and in the midrib region. The position of the midrib is indicated by a region of elongated, thicker walled cells in longitudinal rows. The margin is like that of the upper epidermis. Stomata are numerous on the lower side but absent from the midrib and marginal regions. They are slightly sunken, irregularly orientated and distributed and are almost always separated by ordinary epidermal cells. The guard cells are thinly cutinized except along the edges of the stomatal aperture where there is a thicker rim; the aperture is elongated. Subsidiary cells, usually six in number, form a ring and are generally smaller than the other epidermal cells. They have thicker cuticle on the periclinal walls which forms a ring round the stoma but are not thus thickened adjacent to the stomatal pit. Encircling cells are occasional and unspecialized. Trichomes are absent.

DISCUSSION. The preservation is good though the surface is somewhat cracked and because of the shortage of material available only a little could be macerated.

However, it was established that the specimen is attached to the rock by its upper surface and that whilst the lower cuticle is complete most of the upper is missing, only a narrow strip remaining around the edge of the pinnules. Thus very little upper cuticle has been examined and it is not known whether it had any stomata nearer the middle of the pinnule. Only a few of the pinnules show the positions of the midrib and the laterals on the underside, and at best they are indistinct. An attempt was made to see the venation by transmitted light during maceration but this failed. The prepared cuticle, whilst showing the position of the midrib by the elongated cells and lack of stomata, gives no indication of the position of the lateral veins.



FIGS. 45–47. *Pachypteris lanceolata* Brongniart. 45. Part of pinna showing venation. V.3145. × 4. 46. Reconstructed transverse section of pinna showing prominent rachis on lower side. ×4. 47. A single stoma. The darker stippling indicates the ring of thicker cuticle. Slide V.3145*b*. × 700.

The surface of the specimen viewed in reflected light shows very clearly the cells of the lower epidermis with a divergent trend in relation to veins. In the fragmentary cuticle preparations this trend is not apparent and the cells appear haphazard in arrangement. One very prominent cell was seen, the nature of which is obscure though it is certainly not stomatal. It is possibly a trichome base though no similar cells could be identified with certainty.

COMPARISON. A careful comparison was made with specimens of *Pachypteris lanceolata* Brongn. from the Yorkshire Jurassic (Harris 1964). The Yorkshire material is known in much more detail, numerous specimens being available some of which are complete leaves. A notable feature of *P. lanceolata* is its wide range in form with intergradation between the extreme types. These include forms with small oval pinnules, others with small narrow pinnules and much larger forms with lanceolate pinnules. Forms just like the present specimen occur. The cuticles of the various forms although basically the same show a certain variety in details such as number and size of stomata. Some have a large number of stomata close together while in others they are more widely spaced. The cuticle of the present fossil shows more widely spaced stomata than most of the specimens attributed by Harris to *P. lanceolata* but some of the latter approach the Wealden form very closely. These include specimens from Boulby Alum Quarry, Shale 2B; Whorlton, Scugdale, Rank Crag Soft Jet and Eston Moor, Beacon Quarry. It should be pointed out that these are not ordinary specimens but merely cuticle fragments obtained by maceration and identified on their microscopic characters.

As in the Wealden fossil, the stomata of the Jurassic *P. lanceolata* avoid the midrib and margins and are indistinguishable in structure. There is also very close similarity in size and shape of the ordinary epidermal cells, indeed some of the cuticle fragments of the two fossils could scarcely be told apart.

What little is known of the venation of the Wealden form simply affords more evidence of the similarity between these two fossils and consequently I have placed the Wealden specimen in the same species.

GYMNOSPERMAE

CYCADALES

Genus *NILSSONIA* Brongniart

Nilssonia schaumburgensis (Dunker)

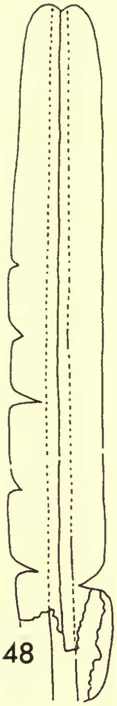
Text-figs. 44, 48–52

Selected references:

1846 *Pterophyllum schaumburgense* Dunker : 15, pl. 1, fig. 7; pl. 2, fig. 1; pl. 6, figs. 5–10.
1871 *Anomozamites schaumburgense* (Dunker) Schenk : 231, pl. 33, figs. 1–9.
1890 *Nilssonia cf. schaumburgensis* (Dunker) Nathorst : 5, 9, 13, pl. 1, figs. 6–9*a*.
1895 *Nilssonia schaumburgensis* (Dunker); Seward : 53, text-fig. 3.
1905 *Nilssonia schaumburgensis* (Dunker); Fontaine *in* Ward : 303, pl. 72, figs. 17–21.

EMENDED DIAGNOSIS. Leaf linear; width usually 3–5 mm., rarely up to 12 mm.; length unknown but at least 9 cm. Apex rounded and notched; base tapering. Midrib 1–2 mm. wide, depressed on upper surface, depression not narrowing towards apex. Lamina entire or more or less divided. Surface of lamina flat or slightly convex upwards. Veins fairly prominent, projecting above and below; arising from midrib at an angle between 70° and 80°; concentration of veins typically three to four per mm.

Cuticle of moderate thickness but anticlinal walls often obscure. Marginal cells of leaf and pinnae elongated parallel to edges and having thicker and more distinct anticlinal walls. Cells in main part of lamina tending to be elongated almost at right angles to edge, parallel with veins. Upper cuticle without stomata or trichomes, positions of veins scarcely distinguishable. Lower cuticle not showing positions of veins clearly but cells with slight tendency to be more elongated over veins. Stomata scattered between veins; small, inconspicuous and scarcely sunken.



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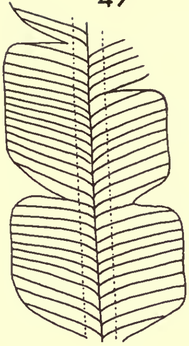

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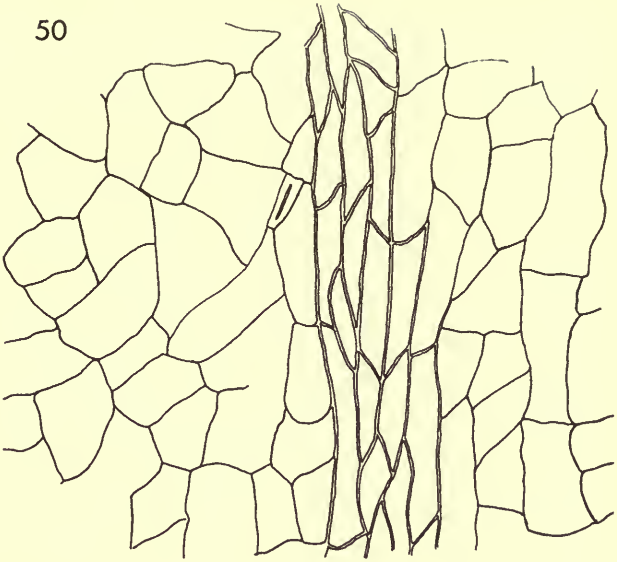

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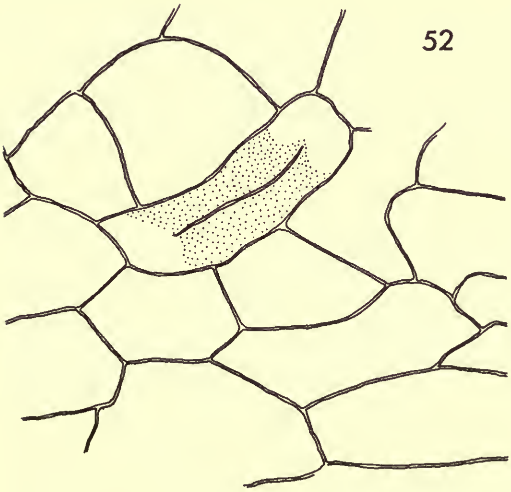

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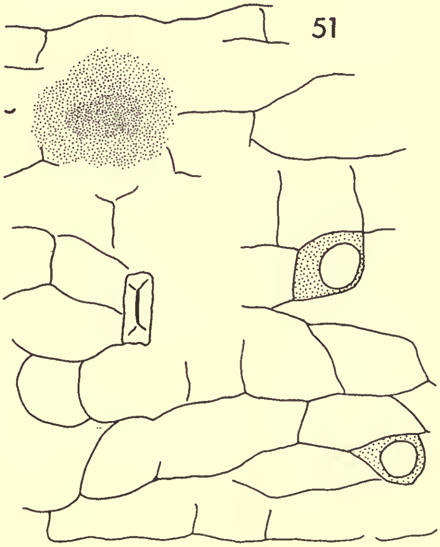

FIGS. 48–52. *Nilssonia schaumburgensis* (Dunker). 48. Leaf, slightly divided, showing form of apex. Position of rachis indicated by dotted line or solid line where lamina is broken and rachis is exposed. V.3762. × 2. 49. More divided leaf showing the veins. Position of rachis shown by dotted lines. V.2171. × 5. 50. Cuticle showing elongated cells of leaf edge in centre, lower surface to the left, upper surface to the right. Slide from V.1436. × 300. 51. Lower cuticle showing a resin body, a stoma and two single-celled trichome bases. Slide from V.2171**. × 300. 52. Single stoma showing exposed guard cells. Slide from V.3762. × 700.

Guard cells exposed; 30–50 μ long and about 15 μ wide, surrounded by several unspecialized and ill-defined subsidiary cells. Unicellular trichome bases scattered over whole lower surface; thickly cutinized except for central circle. Resin bodies occasionally seen, about 50 μ across. Reproductive organs unknown.

Description. This small *Nilssonia* is represented by more than a dozen specimens from the English Wealden. They show a good deal of variety in the form of the lamina, some being entire, others slightly and irregularly divided, others regularly and completely divided almost to the midrib. Only two specimens are more than 6 mm. wide, V.2171*a* which is 12 mm. wide (Seward 1895 : 53, text-fig. 3*c*) and V.3731 which Seward labelled as *Taeniopteris beyrichii* var *superba*. Both agree with the others in their cuticle. All but one specimen have the adaxial surface exposed and in these the midrib is seen only when the substance of the lamina is broken away (Text-fig. 48) but in all specimens its position is indicated by a depression of the lamina. This depression retains its width to the apex of the leaf. V.3731 is the only specimen with the lower surface uppermost and is the largest specimen, 9 cm. long (incomplete) and 11 mm. wide, tapering to 4 mm. near the base. The rachis is 2·5 mm. wide whilst in most specimens it is little more than 1 mm.

Resin bodies are rare; they are not seen on the surface of the fossils and only three were seen in macerated cuticle fragments.

The stomata are particularly difficult to distinguish and were identified with certainty on only a very few pieces of lower cuticle. The stoma in Text-fig. 52 is the best example seen and shows a slight surface thickening in the middle region of the guard cells.

Discussion. *Nilssonia schaumburgensis* has been identified by numerous authors from several countries. In all cases there is very little detail on which to compare the various accounts. From the few details available, i.e. size, shape and vein concentration the English material agrees well with the type-material described by Dunker (1846) and the specimens figured by Schenk (1871), Nathorst (1890) and Fontaine *in* Ward (1905).

Comparison. *N. revoluta* Harris (1964) from the Jurassic (Upper Deltaic) of Yorkshire is the only other species I know which is as small as *N. schaumburgensis*. The leaves are similar in size and are entire; also the vein concentration is similar, up to thirty per cm. Another similarity is that the veins are scarcely shown in the upper cuticle, however they are strongly indicated in the lower cuticle. Rather different characters shown by *N. revoluta* include conspicuous cell outlines with nodular thickenings and bulging subsidiary cells.

Genus **BECKLESIA** Seward 1895 : 179

Becklesia anomala Seward

Text-figs. 53–56

1895 *Becklesia anomala* Seward : 179, pl. 14, figs. 2, 3.

Emended diagnosis. Leaf simply pinnate, probably much longer than broad (whole leaf unknown), consisting of a slender rachis bearing two lateral rows of long straight pinnae. Rachis 6 mm. wide, pinnae arising at intervals of approximately 1 cm., at an angle of about 40°. Pinnae at least up to 10 cm. long, 3 mm. wide, narrowing to about 2 mm. near rachis (apex unknown), rounded in transverse section; margins of pinnae straight. Lower side of pinna having broad, flat midrib

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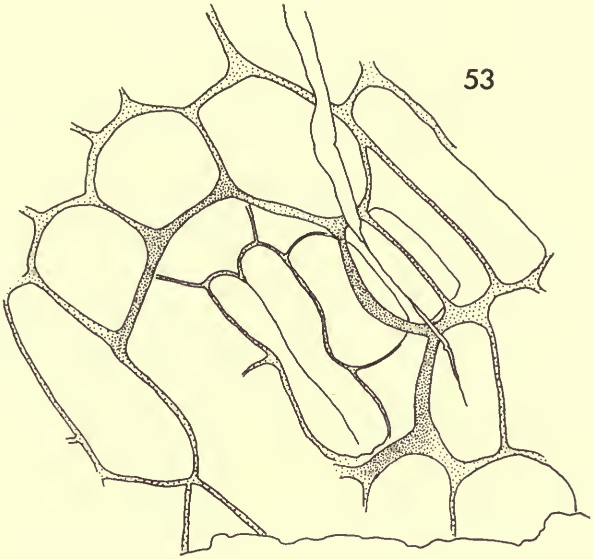

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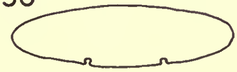

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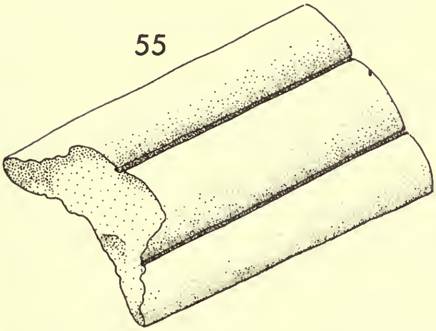

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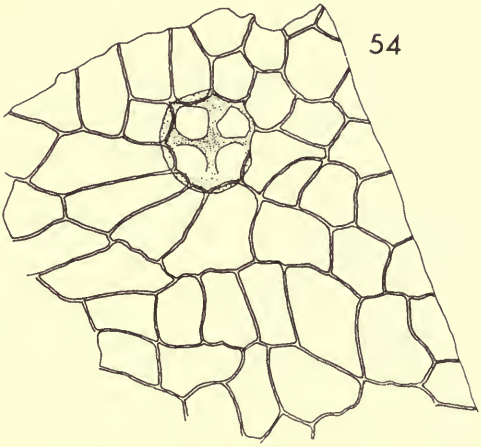


Figs. 53–56. *Becklesia anomala* Seward. 53. A single stoma. One hypodermal cell is seen on the right indicated by a single line; Slide from V.2361*a*. × 700. 54. A piece of cuticle from a non-stomatal region of the leaf, showing a four-celled trichome base. Slide from V.2361*a*. × 200. 55. An unsquashed portion of the pinna showing the two narrow stomatal grooves on the lower side. V.2361*a*. × 10. 56. A reconstructed section of a pinna. × 10.

flanked by two very narrow, shallow stomatal grooves with lateral non-stomatal regions about as broad as the midrib; upper surface flat but some pinnae showing numerous raised trichome bases.

Cuticle about 2 μ thick in non-stomatal regions, very delicate in stomatal grooves. Ordinary epidermal cells of upper and lower surface large, thin walled and arranged in longitudinal rows; very varied in shape, either square, rectangular or quite irregular; typically 50 μ broad. Cells over midrib and at edges of pinna tending towards diamond shape. Anticlinal walls cutinized, usually straight but sometimes slightly sinuous. Presence of a hypodermis occasionally indicated, particularly near trichome bases. Trichome bases mostly occurring on upper surface but sometimes also in non-stomatal regions of lower surface; roughly circular in surface view, about 60–70 μ diameter, composed of up to four small, thick-walled cells tending to overlap other epidermal cells. Trichome bases not present on all pinnae. Stomata longitudinally orientated and scattered in grooves about 45 μ wide. Guard cells thinly cutinized, about 45 μ long with six to seven subsidiary cells surrounding and slightly overlapping them; guard cells and subsidiary cells slightly sunken in shallow stomatal pit, surrounded by thicker walled cells, inner walls of which form thickly cutinized pit rim. Ordinary epidermal cells between stomata much smaller than those in non-stomatal regions.

HOLOTYPE. V.2361*a*.

DESCRIPTION. This species is described from two specimens both of which are incomplete leaves with no complete pinnae. Whilst most of the pinnae have been squashed during preservation, two fragments are so preserved that they retain their original shape and thickness. One is about 1 mm. thick and shows particularly well that the stomatal grooves are shallow, that the midrib is flat, and that the margin is rounded in section.

Much of the plant substance is missing from the two specimens and what remains is very cracked, so that all cuticle preparations are small pieces. Cuticle from the non-stomatal regions was easily obtained but it was only with considerable difficulty that preparations of the stomatal grooves were made. All grooves are filled with matrix and have extremely delicate cuticle which disintegrates even when most carefully macerated. The stoma shown in Text-fig. 53 is from the best preparation obtained in which, unfortunately, all the stomatal pits contain debris which obscures some of the details.

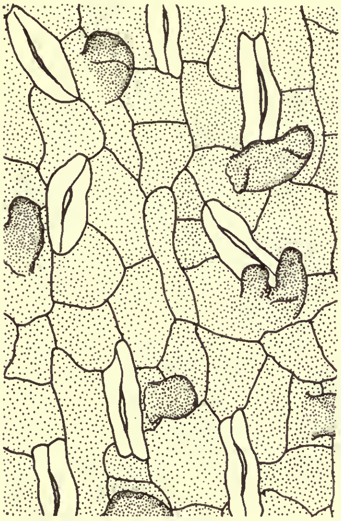
DISCUSSION. While the characters of this species are distinctly Cycadalean it is not closely comparable to any other genus, living or fossil. It is thus convenient to retain the original generic name. The stomatal grooves are much narrower than in any other Cycad. In *Cycas* stomata are present over the whole of the lower surface except the midrib and margins. The trichome bases of *B. anomala* are similar to those in *Cycas revoluta* (Pant & Mehra 1962, text-fig. 33D) but in that species they are two-celled.

Amongst fossil Cycads *Paracycas cteis* Harris (1964) from the Jurassic (Lower Deltaic) of Yorkshire is similar in size but differs in such features as wider stomatal bands and irregularly arranged stomata.

Becklesia sulcata sp. nov.

Pl. 2, fig. 6; Text-figs. 57–58

Diagnosis. Pinnae up to 2 mm. wide (length unknown), with two narrow longitudinal grooves on lower side; stomata confined to these grooves. Grooves so placed that the central non-stomatal region is twice as wide as lateral non-stomatal regions. Margins smooth and entire. Cuticle moderately thick but much thinner in stomatal grooves. Non-stomatal region between grooves composed of cells in longitudinal rows, transverse anticlinal walls usually oblique, sometimes slightly sinuous. Cells of other non-stomatal regions not arranged in rows, very varied in shape and irregular in arrangement; walls often slightly sinuous. Guard cells extremely thinly cutinized, except for slight thickening around stomatal aperture. Guard cells about 50 μ long, not at all sunken, irregularly orientated but majority more or less longitudinal. Subsidiary cells very variable, not distinguished from other ordinary epidermal cells in groove, all of which are irregular in shape and size, smaller than epidermal cells of non-stomatal regions. Subsidiary cells often shared by adjacent stomata. Some of these cells bearing large, hollow, globular or elongated papillae; usually one such papilla near each stoma.



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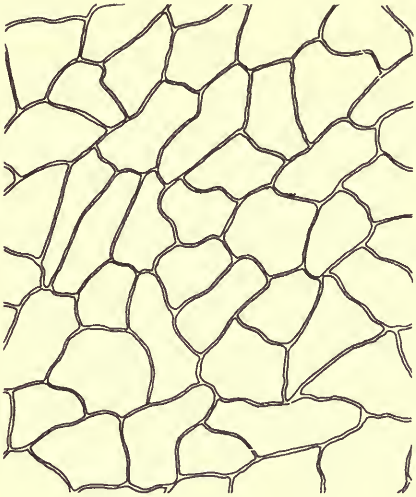

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Figs. 57, 58. *Becklesia sulcata* sp. nov. 57. Cuticle from a stomatal groove showing stomata and papillae. Holotype, V.51524. × 300. 58. Cuticle of upper side. V.51524. × 300.

Holotype. V.51524.

Description. This species is known only from cuticle fragments which are assumed to be pieces of pinnae although there is no direct evidence that they are from a pinnate leaf. However, it is so similar to *Becklesia anomala* Seward that I have placed it in the same genus. The main similarities are in such features as width of pinnae, position and width of stomatal grooves and form of ordinary epidermal cells.

Comparison. *Becklesia sulcata* lacks the multicellular trichome bases of *B. anomala*, has thinner more exposed guard cells and has large papillae.

If the form of ordinary epidermal cells is any criterion in considering the affinities of these little known plants, these irregular yet characteristic cells are almost exactly the same as in many living Cycads e.g. *Cycas revoluta*.

GINKGOALES

Genus ***PSEUDOTORELLIA*** Florin 1933 : 142

Emended diagnosis. Leaves entire, linear to elliptic; apex rounded, narrowing at base. Two or more longitudinal veins formed by dichotomies chiefly in basal part, ending blindly. Stomata confined to lower side, always longitudinally orientated; haplocheilic, monocyclic or incompletely amphicyclic; guard cells sunken, strongly cutinized. Subsidiary cells four or more. Epidermal cells with straight or faintly sinuous outlines.

The new fossil described here is at least the ninth species of this genus to be described and it now seems necessary to emend the generic diagnosis as the original diagnosis is too narrowly defined for present purposes, based as it was on the single species *P. nordenskioldi* Florin. The simplified, broader diagnosis above will better serve to admit such a fossil as the new English Wealden species with its wide range of leaf form and scattered stomata.

Type species. *Pseudotorellia nordenskioldi* Florin 1933.

Pseudotorellia heterophylla sp. nov.

Pl. 6, figs. 6, 7; Text-figs. 59–64.

Diagnosis. Leaves entire, showing wide range of size and shape from narrow and needle-like to broad and elliptic. Dimensions of holotype 12 mm. long and 3 mm. wide; longest leaf known 3 cm. long and 1 mm. wide; other leaves ranging between these two. Apex unknown. Petiole unknown.

Veins varying in number from two in narrowest leaf to eight in broadest, formed by dichotomies near base of leaf. Veins may converge near apex but end blindly. Interstitial ducts sometimes present between veins.

Cuticle thick and leathery. Stomata present on one side of leaf only, scattered over whole surface (presumably lower), not avoiding veins; longitudinally orientated, typically 80 μ long. Ordinary epidermal cells elongated, arranged in longitudinal rows, sometimes with elongated, thickened ridge along surface. Surface of cuticle frequently sculptured.

Guard cells sunken beneath subsidiary cells, strongly thickened at common junction wall with overlying subsidiary cells. Subsidiary cells six, usually papillose, papillae projecting over stomatal aperture. Stomata usually not upsetting sequence of cell rows, subsidiary cells continuous in their lines of ordinary epidermal cells. Sometimes small subsidiary cells coinciding with outer edge of guard cells, forming ring or partial ring of more specialized subsidiary cells. Encircling cells rare. Guard cells sometimes having long polar appendages.

Upper epidermis without stomata, composed of longitudinal rows of elongated cells with fairly thick walls, sometimes in " packets ", often having finely sculptured cuticle. Positions of veins not indicated on upper surface. Edges of leaf smooth with fairly thick rim of cuticle. Cuticle of all forms of leaf closely agreeing; only minor differences in size of stomata, degree of thickening and form of polar appendages of guard cells.

HOLOTYPE. V.51525.

DESCRIPTION. A considerable number of whole and broken leaves were obtained by bulk maceration of the same coaly material which yielded *Becklesia sulcata*. Besides these a few of the larger needles were picked off specimen V.2222 in the British Museum (Natural History) collections. Several fragments were also identified in washings from the core of a borehole drilled near Winchester. Most of the linear leaves were found only in short lengths whilst the large elliptical leaves were almost whole. However, on none of these is an apex or petiole present. The petiole presumably had one vein which dichotomized at the base of the leaf to give the two main veins which may further give off branches on their inner sides in the lower part of the leaf. The veins are then parallel along the length of the leaf but may converge slightly near the apex (Text-figs. 61, 62.) although they all appear to end blindly. The interstitial ducts which are often present between veins are of unknown nature but are possibly resin ducts or even subsidiary veins.

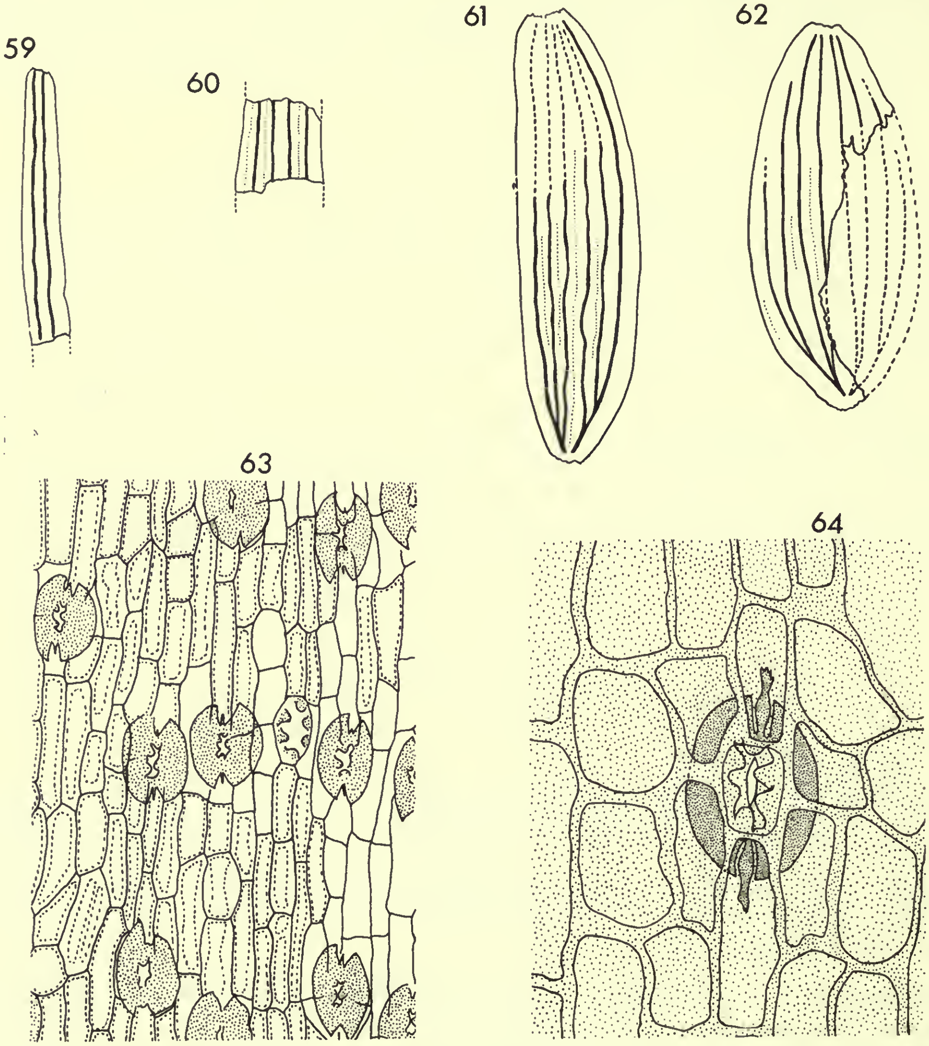
A number of leaves have what appear to be abortive stomata. One of these is seen in Text-fig. 63. No guard cells are developed but a ring of papillae surround the " guard cell mother-cell ". A few other " freak " stomata were seen where the guard cells were misplaced under the stomatal pit. Only one transversely orientated stoma was seen.

The differences in polar appendages of guard cells may be compared in Text-figs. 63, 64. Text-fig. 64 shows a stoma with the longest and most complex appendages projecting well beyond the ends of the guard cells. In Text-fig. 63 the appendages are quite short and pointed or scarcely developed at all. Also shown in Text-fig. 63 are some stomata with the subsidiary cells following the line of the guard cells as mentioned in the diagnosis.

COMPARISON. *P. heterophylla* shows a much wider range of leaf form than other species. *P. nordenskioldi* (Nathorst) described by Florin (1933), *P. minuta* (Nathorst) by Lundblad (1957), *P. ensiformis* (Heer) and *P. crassifolia* (Prynada) by Doludenko (Vachrameev & Doludenko 1961) all have the greatest width of their leaf situated towards the apex. *P. grojecensis* Reymanówna (1963), *P. ephela* (Harris 1935) and the elliptic leaves of *P. heterophylla* have the greatest width of the leaf situated in the middle region. *P. angustifolia* Doludenko and *P. longifolia* Doludenko

(Vachrameev & Doludenko 1961) both have long linear leaves of similar dimensions to some forms of *P. heterophylla*.

A common feature of the *Pseudotorellia* cuticle is the presence of median ridges of cuticle on the epidermal cells. *P. heterophylla*, *P. nordenskioldi*, *P. minuta*, *P. ephela* and *P. ensiformis* all have these ridges. In all, the epidermal cells are similar in form, longitudinally elongated. The packets of cells seen in the upper epidermis



FIGS. 59–64. *Pseudotorellia heterophylla* sp. nov. 59–62. Various forms of leaf showing veins. Figs. 60–62 showing interstitial ducts. Fig. 59, V.51526, Fig. 60, V.51527, Fig. 61, Holotype, V.51525, Fig. 62, V.51528. All × 10. 63. Cuticle showing stomata, abortive stoma and ridges on the epidermal cells. V.51529. × 150. 64. Stoma with long polar appendages. Slide from V.2222. × 300.

of *P. heterophylla* (Pl. 6, fig. 6) are surpassed in development by those seen in *P. grojecensis*. In that species the packets consist of up to five cells and form a conspicuous pattern at right angles to each other (Reymanówna 1963, text-fig. 8A.)

The stomata of *P. heterophylla* appear to be more heavily cutinized than in other species. For instance in *P. ephela* and *P. grojecensis* the guard cells are heavily cutinized at the outer edges and along the stomatal aperture but in *P. heterophylla* the whole upper surface of the guard cells is heavily cutinized, but sometimes slightly thinner around the aperture.

The polar appendages of *P. heterophylla* are unique among the species under consideration for the rest have thin polar areas.

Papillate subsidiary cells like those in *P. heterophylla* are also present in *P. ephela*, *P. minuta* and *P. ensiformis* while *P. grojecensis* has a cuticular diaphragm on the surface of the guard cells around the aperture.

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EXPLANATION OF PLATES

Most of the figured specimen, are in the British Museum (Natural History) and bear the prefix V.

PLATE 1

Circonitella knowltoni (Seward)

FIGS. 1, 2. Gyrogonites showing five spiral cells meeting at the apical pole. Fig. 1, V.51552, Fig. 2, specimen lost. × 80.

FIG. 3. Basal pole of gyrogonite showing circular basal plate. V.51553. × 80.

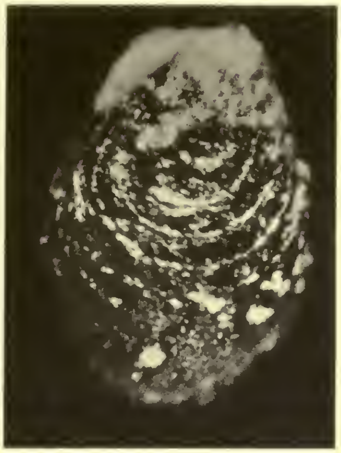
FIG. 4. Pyritised, unsquashed gyrogonite with convex spiral cells, showing basal plate. V.51554. × 80.

FIG. 5. Neotype with convex spiral partly broken away. V.51555. × 80.

FIGS. 1–5, individual specimens all from one block numbered V.51548 (re-registered from V.1070*a*).

Pachypteris lanceolata Brongniart

FIG. 6. Apical part of pinna, lower side uppermost, showing prominent midrib. V.3245. × 2.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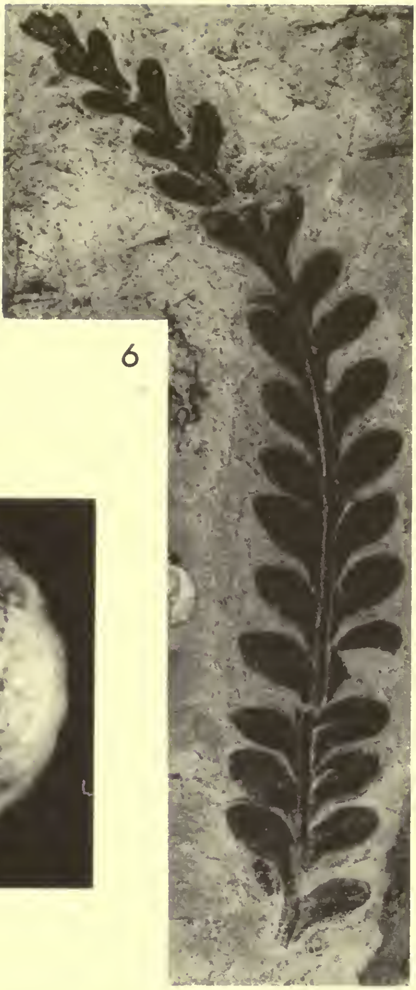
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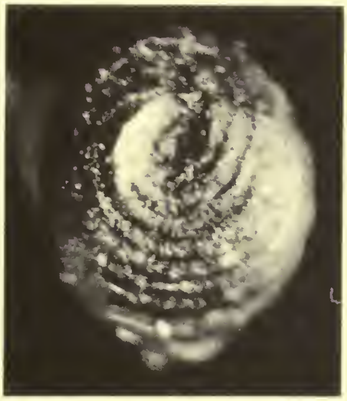
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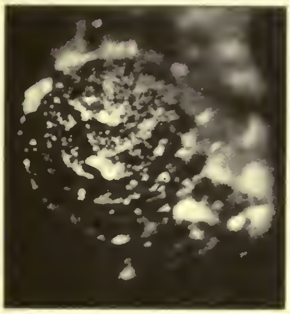
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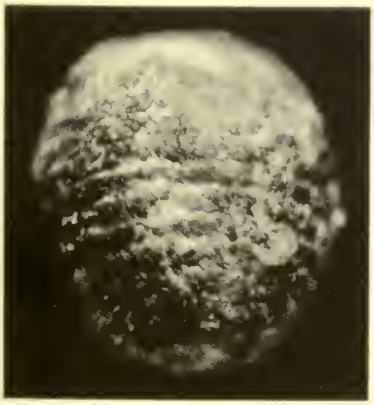
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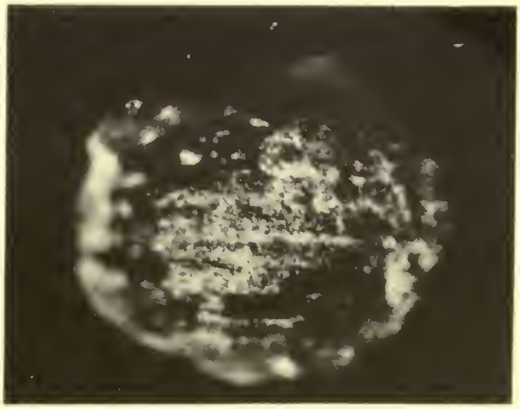
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PLATE 2

Hepaticites zeilleri (Seward)

FIG. 1. General form of thallus showing dichotomous branching. Holotype, V.2330*a* × 1.

FIG. 2. Thallus showing thick midrib region and delicate lamina also rhizoids including detached bunches. V.2330*a*. × 3.

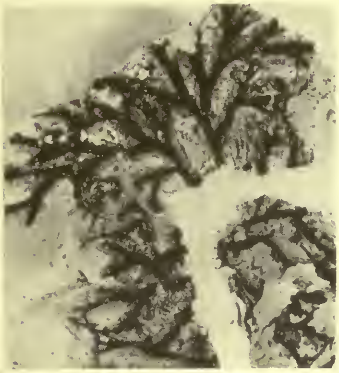
FIG. 3. Enlargement showing rhizoids pointing forwards between a dichotomy of the thallus. V.2330*a*. × 10.

Hepaticites ruffordi sp. nov.

FIGS. 4, 5. Thallus showing arcuate grooves, Fig. 4 immersed in paraffin, Fig. 5 coated with ammonium chloride. Holotype, V.2343. × 3.

Becklesia sulcata sp. nov

FIG. 6. Part of a pinna showing stomatal grooves. V.51540. × 20.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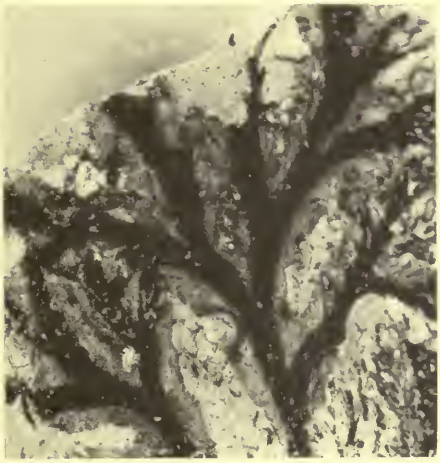
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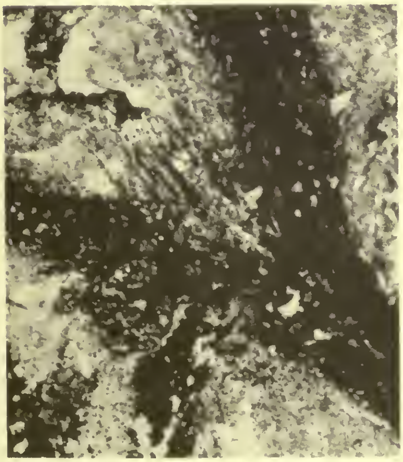
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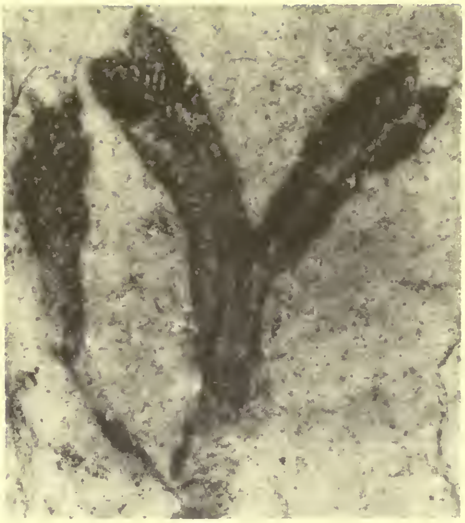
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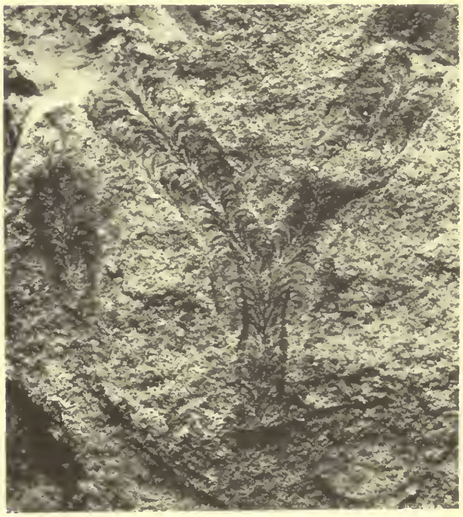
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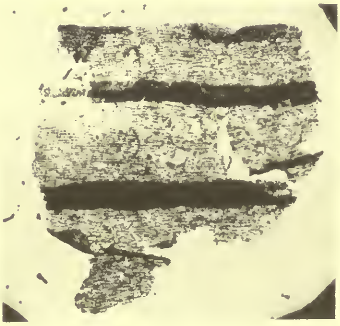
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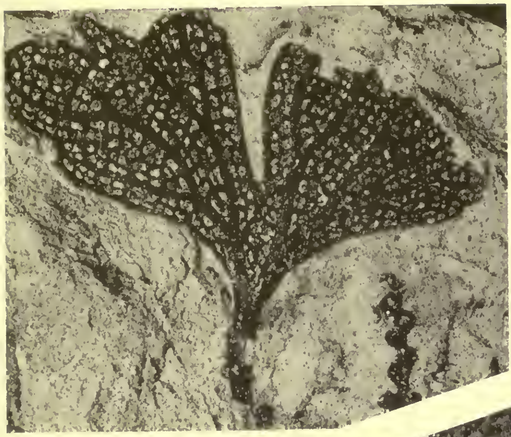
PLATE 3

Hausmannia dichotoma Dunker

FIG. 1. Small fan-shaped leaf with broken apices. Sterile. V.12317. × 3.

FIG. 2. Larger more divided leaf with strap-shaped segments. Sterile. V.12349. × 3.



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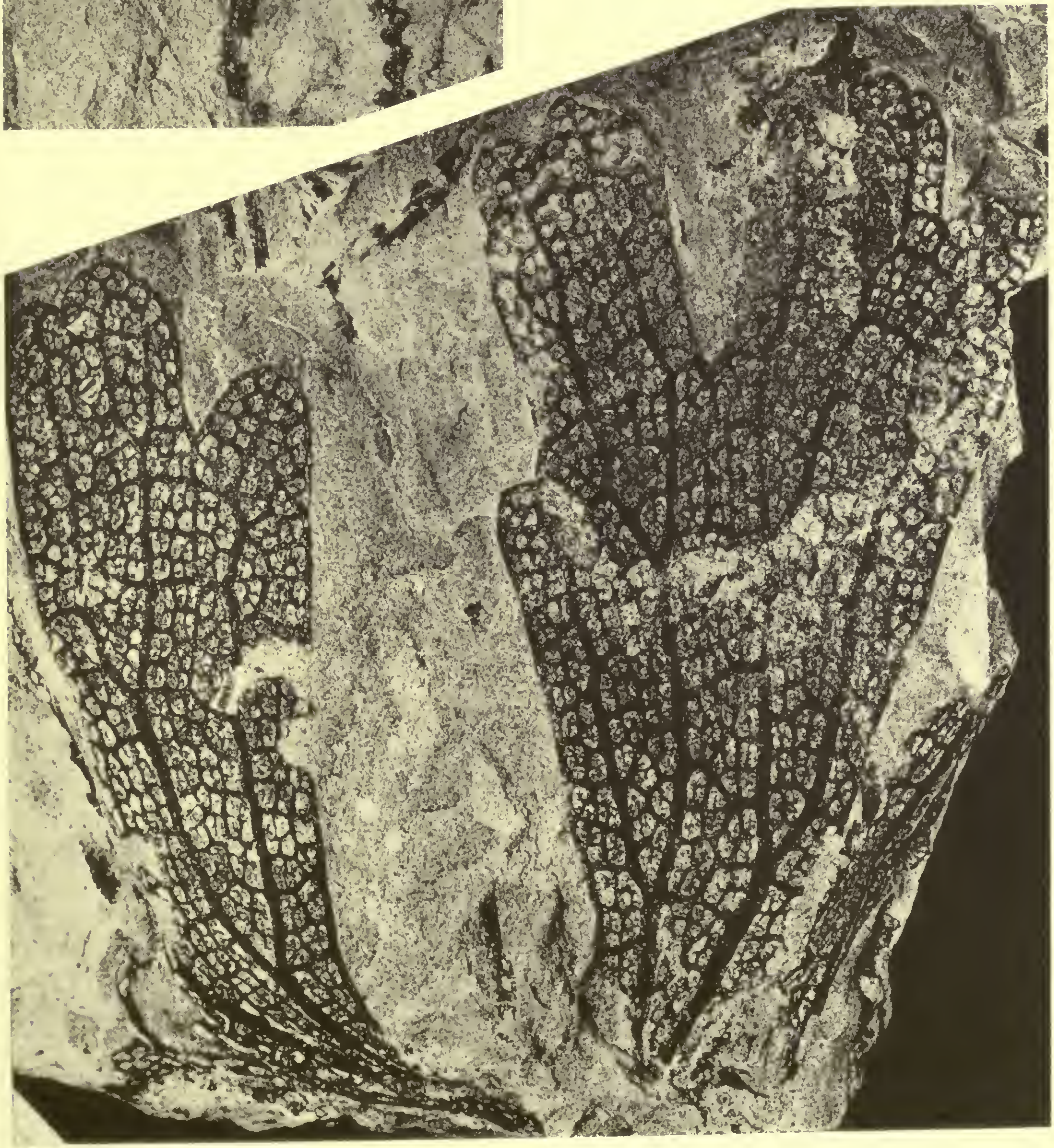


PLATE 4

Ruffordia goepperti (Dunker)

FIG. 1. Frond with narrowest form of segments. V.2157. × 1.

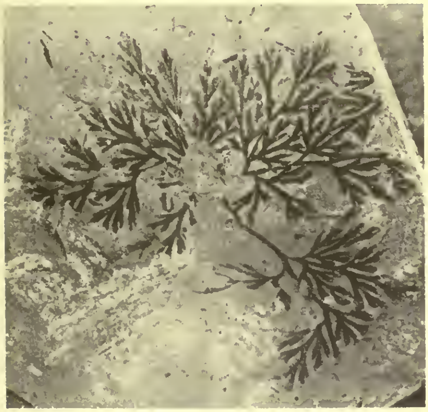
FIG. 2. Frond with wider sterile pinnules at the top. Fertile pinnae at the base scarcely visible (photographed dry). V.2295. × 1.

FIGS. 3, 4. Fronds with widest pinnules. Fig. 3, V.2357. ×1. Fig. 4, V.12331. ×1.

FIG. 5. Part of V.2157. × 3.

FIG. 6. Sterile part of V.2295. × 3.

FIG. 7. Pinna of V.2357 showing ventation. × 3.



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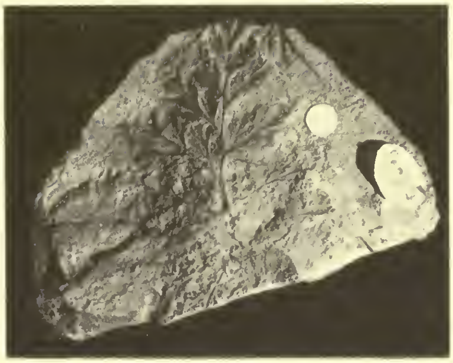

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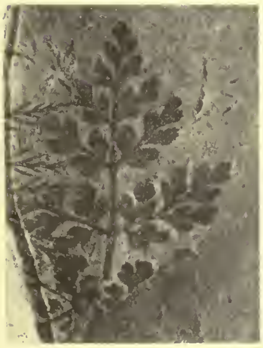

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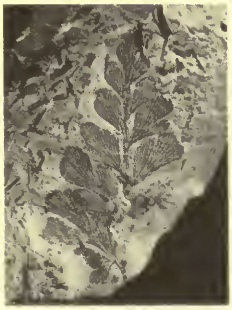

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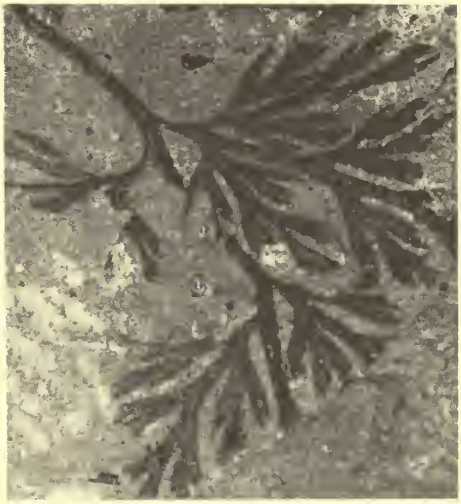

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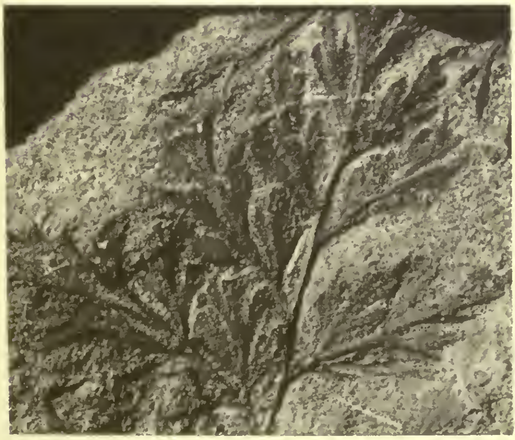

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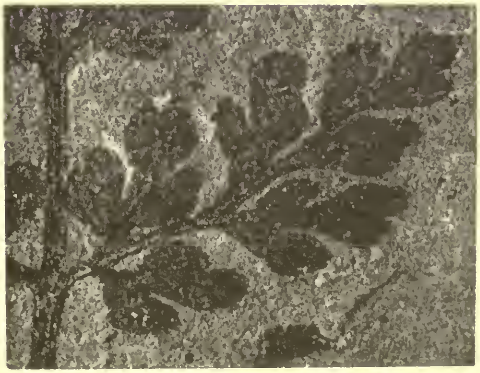


PLATE 5

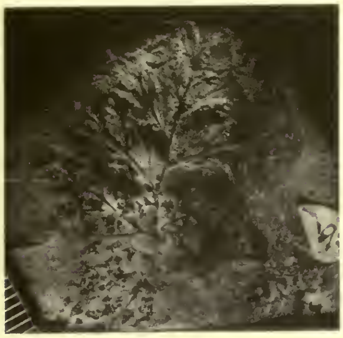
Ruffordia goepperti (Dunker)

FIG. 1. Specimen with sterile top and fertile base, immersed in paraffin. V.2295. × 1

FIG. 2. Fertile frond. V.2160. × 1.

FIG. 3. Fertile frond. V.2192*a*. × 1.

FIG. 4. Frond in Fig. 3 enlarged to show the undulating margins of the fertile pinnules. V.2192*a*. × 3.



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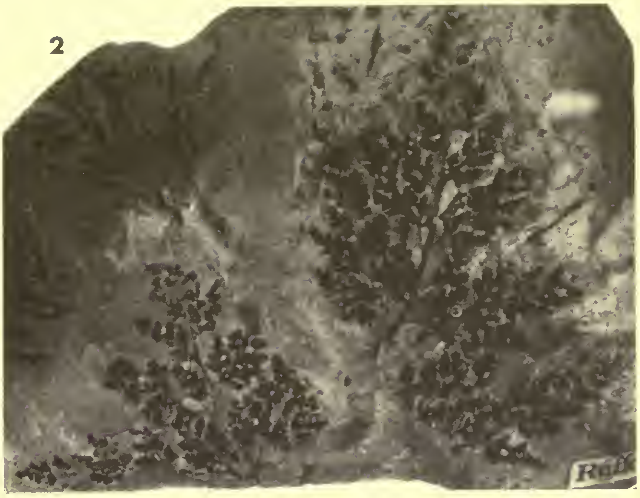

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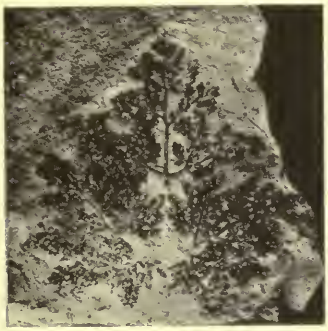

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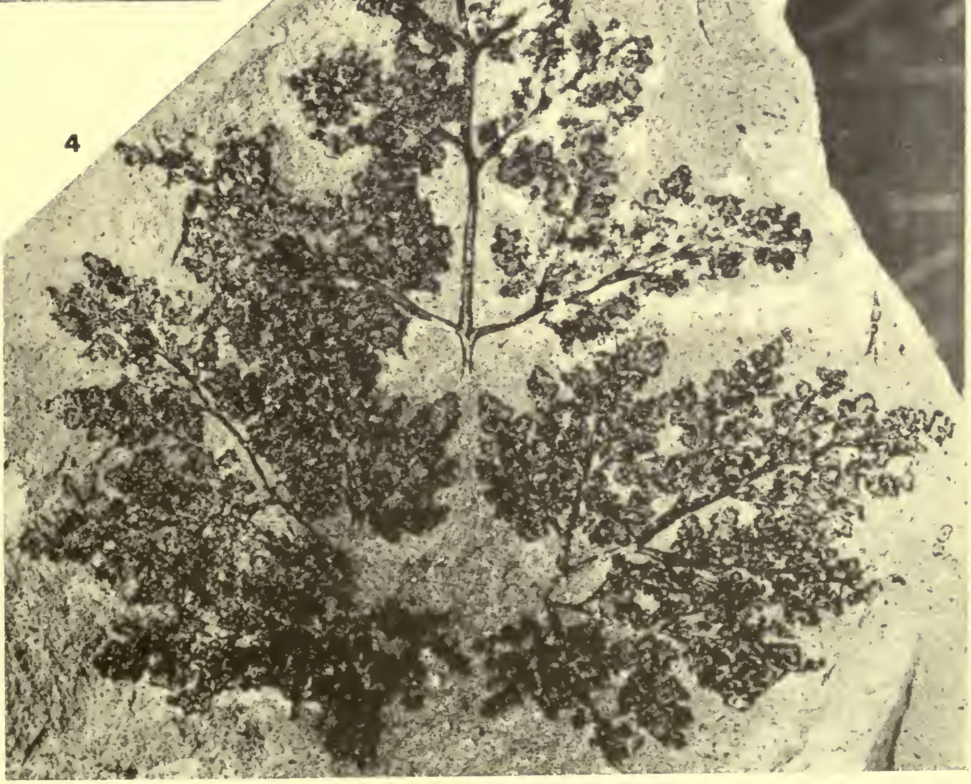

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PLATE 6

Pelletieria valdensis Seward

FIGS. 1, 2. Largest fertile specimen picked out of the matrix. V.2368. Fig. 1, × 1, Fig. 2, × 3.

Aspidistes sewardi sp. nov.

FIG. 3. Specimen immersed in paraffin, sori visible on most of pinnules. Holotype, V.2173*a* × 1.

FIG. 4. Middle part of same specimen enlarged to show rachis, sori and rolled edges. × 3.

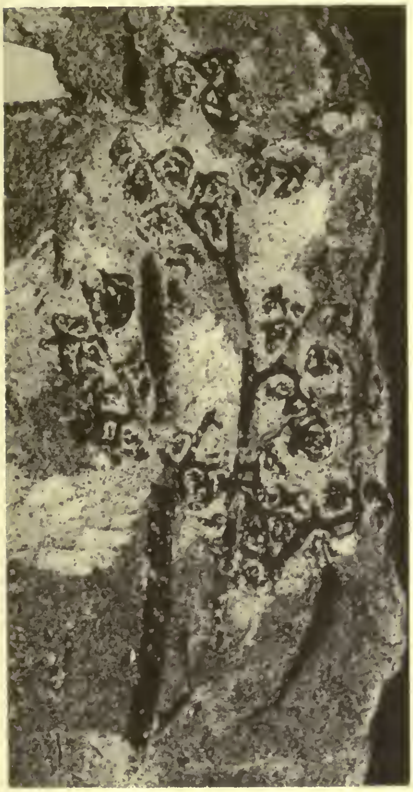
Weichselia reticulata (Stokes & Webb)

FIG. 5. Part of pinna showing typical form with fleshy pinnules. Indication of reticulate venation just visible in two bottom-left pinnules. V.2174*a*. × 3.

Pseudotorellia heterophylla sp. nov.

FIG. 6. Cuticle of upper surface showing cells in " packets ", Geological Survey & Museum PF 2758, × 200.

FIG. 7. Cuticle of upper surface from same specimen showing sculptured surface of the cells, × 500.



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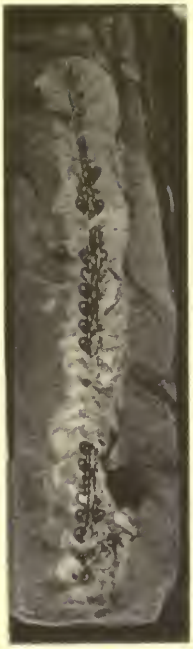

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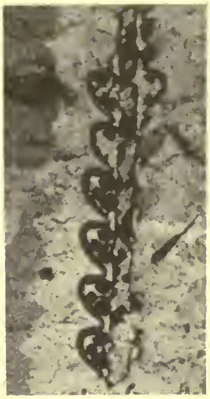

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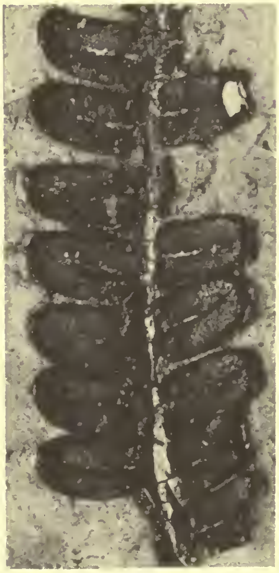

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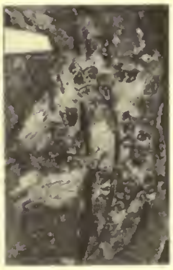

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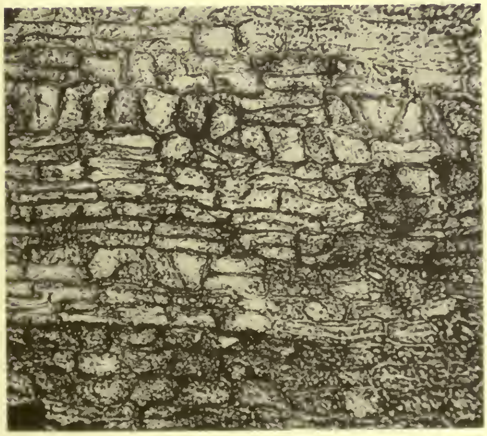

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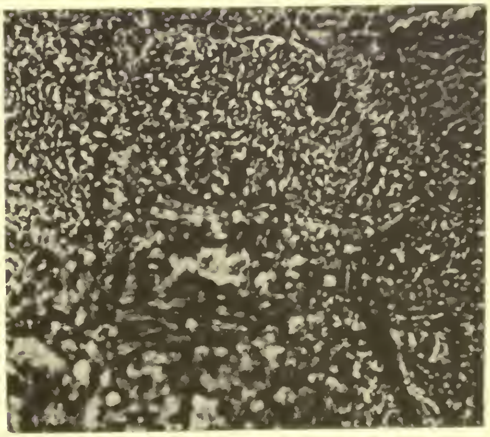

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BARTHOLOMEW PRESS, DORKING

TWO NEW DICYNODONTS FROM THE TRIASSIC NTAWERE FORMATION, ZAMBIA

C. B. COX

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
GEOLOGY Vol. 17 No. 6
LONDON: 1969

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NATURAL HISTO

TWO NEW DICYNODONTS FROM THE TRIASSIC NTAWERE FORMATION, ZAMBIA

BY

C. B. COX Xref
Department of Zoology, King's College, London

Pp. 255–294; 23 *Text-figures*

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THE BULLETIN OF THE BRITISH MUSEUM (NATURAL HISTORY), *instituted in* 1949, *is issued in five series corresponding to the Departments of the Museum, and an Historical series.*

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This paper is Vol. 17, *No.* 7 *of the Geological Palaeontological series. The abbreviated titles of periodicals cited follow those of the World List of Scientific Periodicals.*

World List abbreviation:
Bull. Br. Mus. nat. Hist. (Geol.).

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Issued 7 March, 1969 *Price Seventeen Shillings*

TWO NEW DICYNODONTS FROM THE TRIASSIC NTAWERE FORMATION, ZAMBIA

By CHRISTOPHER BARRY COX

CONTENTS

		Page
I.	HISTORICAL INTRODUCTION	257
II.	STRATIGRAPHY	258
III.	SYSTEMATIC DESCRIPTIONS	260
	Genus *Zambiasaurus submersus* nov.	262
	Genus *Sangusaurus edentatus* nov.	286
IV.	AGE OF THE NTAWERE FAUNAS	290
V.	ACKNOWLEDGMENTS	293
VI.	REFERENCES	293

SYNOPSIS

Two new types of dicynodont from the upper fossiliferous horizon of the Ntawere Formation of Zambia are described. The first, *Zambiasaurus submersus*, is represented by the fragmentary remains of at least eighteen juveniles and one adult, all of which were apparently drowned in a sudden flood. *Zambiasaurus* is a stahleckeriid closely related to, and probably directly ancestral to, *Stahleckeria* of the Middle Triassic of Brazil. It is the earliest known stahleckeriid, and the first known outside South America. The earlier history of the group is unknown.

The other new dicynodont, *Sangusaurus edentatus*, is known only from a few fragments of the skull. It is a kannemeyeriid, and shows some similarities to *Ischigualastia* of the Middle or Upper Triassic of Argentina.

Both the faunas of the Ntawere Formation appear to be intermediate in age between the Cynognathus Zone fauna of South Africa and the Manda fauna of East Africa. Its age, in terms of the standard Triassic sequences, is provisionally estimated as lowermost middle Triassic (Lower Anisian).

I. HISTORICAL INTRODUCTION

THE Luangwa River is a major tributary of the Zambezi River, and is the main river of the eastern half of Zambia. Fossil reptiles were first found in the upper Luangwa River valley by Prentice in 1925, and the area was reconnoitred and later investigated by Dixey in 1928 and 1935 (see Dixey 1936, 1937). He recorded fossil reptiles from six different horizons within the Karroo succession, and also from a higher horizon which he named the " Dinosaur Beds " and which he regarded as Cretaceous in age.

The upper Luangwa River valley is remote, and is inaccessible to vehicles unless these can negotiate rough dirt tracks. As a result, the area was not re-examined until 1960 and 1961, when Dr. A. R. Drysdall of the Geological Survey of Northern Rhodesia, and James Kitching, Field Officer of the Bernard Price Institute for Palaeontological Research of Witwatersrand University, spent a total of four months in the area. They examined the area north-west of the small village of Sitwe, on the River Luwumbu, 125 miles north of Lundazi, the administrative centre of this north-eastern portion of the Eastern Province of Zambia. They confirmed that the area was rich in fossil reptiles, and collected nearly 500 specimens.

Karroo fossils were, of course, originally found in South Africa, and many of the early specimens were sent to the British Museum (Natural History) in London for appraisal and description. The resulting collection is of historic interest and contains many type specimens, but many are imperfect and most of them are poorly documented and lack post-cranial elements. It was therefore decided to mount a major expedition to Africa, with the aim of making a large and representative collection of fossil Permian and Triassic vertebrates, using up-to-date methods of collecting and recording full details as to their localities and stratigraphical origin. In view of the known richness of the area, it was decided to rely upon the upper Luangwa River valley for the collection of the bulk of the Permian fossils, and afterwards to visit the south-western region of Tanganyika, where fossil vertebrates of both Permian and Triassic age were known to occur.

The resulting expedition, the British Museum (Natural History) and University of London Joint Palaeontological Expedition to Northern Rhodesia and Tanganyika, spent six weeks collecting in the Sitwe area in the summer of 1963, and a preliminary account of the results has been published (Attridge, Ball, Charig & Cox 1964). The expedition was greatly helped by the presence of James Kitching, whose services had been very kindly loaned by the Bernard Price Institute. As a result there was no difficulty in finding the fossil localities, once the necessary tracks for vehicle access had been constructed, and a total of 220 specimens, weighing some 2½ tons, was collected.

II. STRATIGRAPHY

As a result of their examination in 1960–61, Drysdall & Kitching were able to give a detailed account of the stratigraphy and geology of the area (Drysdall & Kitching 1963), from which the details in this section are taken.

Some alterations to Dixey's earlier interpretation of the stratigraphy of the area became necessary. Drysdall & Kitching found that all of Dixey's six Karroo horizons were part of a single richly fossiliferous formation, which they named the Madumabisa Mudstone. The fauna of this is identical with that of the Lower Beaufort Endothiodon and Kistecephalus zones of South Africa.

Above the Madumabisa Mudstone, and separated from it by an hiatus of probably minor nature, Drysdall & Kitching defined a major lithological unit which they have subdivided to give three formations of more convenient thickness. The lowest, the Escarpment Grit, is of varying thickness (230– over 700 feet), whilst the uppermost, the Red Marl, is 230–400 feet thick. Between the two lies the Ntawere Formation, again of varying thickness (400– over 3,500 feet) and consisting of a succession of thin, alternating arenaceous and argillaceous beds. The whole unit is subdivided into formations on the basis of the different proportions of mudstone and grit.

Above the Red Marl lies the non-fossiliferous Upper Grit, over 3,000 feet thick; in some places the two are separated by a thin transition zone of intercalated grits and mudstones, while in others there is a sharp transition.

Drysdall & Kitching found two fossiliferous horizons in the Ntawere Formation and Red Marl. The lower horizon lies within the Ntawere Formation; its fauna consisted predominantly of large dicynodonts, with fairly common large amphibians, and also yielded an excellent *Diademodon* skull which has already been described (Brink, 1963). The upper horizon comprised the uppermost beds of the Ntawere Formation and the lower part of the Red Marl; its fauna contained the remains of both vertebrates and molluscs.

Drysdall & Kitching consider that Dixey's " Dinosaur Beds " can only be identified, both lithologically and geographically, with the fossiliferous Ntawere Formation. Dixey based his assessment of the " Dinosaur Beds " upon some large, fragmentary, rolled bones which he found *in situ* and which Swinton tentatively identified as possibly dinosaurian. However, Drysdall & Kitching found no bones *in situ* at the localities indicated on Dixey's map, but they were able to identify a thin superficial pebble deposit which Dixey regarded as the last débris of the almost completely eroded Dinosaur Beds. This pebble deposit contained large fragmentary bones, mostly identifiable as dicynodont. Bones of comparable size and appearance are common in the nearby Madumabisa Mudstone, so that the bones found in the pebble deposit are probably derived fossils originating in the Madumabisa Mudstone. The bones observed *in situ* by Dixey have not been relocated and may also have been derived fossils. Alternatively they may have come from as yet unrecognized fossiliferous beds of the Ntawere Formation, which is now known to contain pseudosuchians—whose remains are not readily distinguishable from those of dinosaurs.

The fossiliferous beds themselves are dark red, soft mudstones, with feldspathic grit bands. Bones almost always occur individually; no articulated remains have been found. The bones are usually cracked and weathered, suggesting prolonged exposure before burial; they are often covered with a purple-red layer of haematite, or with a thick layer of calcite. Fragments of bone are common in some of the grit bands, and may be the remains of skeletons disarticulated by shortlived floods which were responsible for the coarser sediment forming the grit bands.

Drysdall & Kitching state (1963 : 22) that amphibians and molluscs (*Unio karooensis*) are present towards the base of the upper fossiliferous horizon, where the commonest reptiles are the cynodonts. The cynodonts persist into the higher levels, where the predominant reptile is now a large dicynodont, where the reptiles outnumber the amphibians, and where the molluscs are now rarer. One of the cynodonts has already been described (Brink, 1963) as *Luangwa drysdalli*.

The fossils are found in the systems of small gulleys and eroding flats at the upper ends of the small tributaries of the River Sangu. Each of the dicynodont genera described in this paper was found in an individual collecting area of this kind, within the general area described as " locality 15 " by Drysdall & Kitching, and hence within the upper fossiliferous horizon. During the 1963 expedition we were not able to define the stratigraphic inter-relationships of these individual areas, so that the positions, within this horizon, of the two dicynodont genera described here are not known.

Fossils from the Ntawere Formation are usually fairly scarce and covered with layers of haematite or calcite. The *Zambiasaurus* material makes an outstanding exception to this rule: a portion, about ten yards long and seven yards wide, of the side of a small ridge was found to be strewn with fragments of bone, nearly all of which were completely free from matrix. The whole area was stripped of vegetation and swept clean, with the result that 500–600 fragments of bone were collected. Though no bones could be found *in situ*, some of the fragments were embedded in pieces of coarse, unsorted, highly feldspathic grit. The proportion of the alkali feldspar, quartz and mafic minerals suggests that the parent rock was of granite composition. The poor sorting and lack of rounding of the grains, and unaltered condition of the feldspar, suggests rapid deposition. The whole collection was therefore deposited by one of the floods mentioned above.

III. SYSTEMATIC DESCRIPTIONS

Genus ***ZAMBIASAURUS*** nov.

The new genus has been named *Zambiasaurus* after the new name of its country of origin.

Generic diagnosis: Large dicynodont: the composite restored immature skull is 23 cm. long and 21 cm. broad, while the adult might have had a skull about 45 cm. long and 40 cm. broad. No teeth in upper or lower jaws. Greatest width of skull is across occiput; skull tapers anteriorly. Wide inter-orbital region, narrow inter-temporal region. Blunt snout. Short median suture between nasals. Preparietal bone absent; pineal foramen completely surrounded by parietals. Parietals are slightly concave antero-posteriorly and form bulk of intertemporal bar. No sharp median intertemporal ridge. Interparietal bone does not extend far forwards. Sharp transition between dorsal and occipital surfaces. Occipital wings of squamosal extend laterally and somewhat posteriorly. Palatal surface of premaxilla bears pair of anterior ridges.

At least four sacral ribs. Scapular blade tall and narrow, with low ridge running up antero-external edge; acromion process probably poorly developed. Coracoid foramen wholly within precoracoid bone. Small pubis.

Type species: *Zambiasaurus submersus* sp. nov.

Material: Unless otherwise stated, all specimen numbers refer to the collection deposited in the British Museum (Natural History).

The bone fragments were mainly parts of the post-cranial skeleton. Apart from unidentified fragments and portions of ribs, the collection included:

Vertebral centra	58	Ulna	29
Sacral ribs	7	Ilium	40
Scapula	39	Ischium	16
Coracoid	13	Pubis	9
Precoracoid	4	Femur	51
Clavicle	6	Tibia	24
Sternum	3	Fibula	13
Interclavicle	—	Metapodials, podials etc.	15
Humerus	68	Premaxillae	4
Radius	19	Maxillae	9

Nasals	2	Quadrates	2
Frontals	6	Squamosals	27
Postorbital	1	Dentaries	2
Intertemporal region	8	Articular region of lower jaw	10
Braincase elements	8	Other fragments of lower jaw	6

As found, none of the limb bones was complete, but it was subsequently found that the fragments included the whole of an ulna, two femora and two tibiae. Apart from a few cynodont bones, and one other exception discussed below, there is no variation in the morphology of the bones, which therefore appear all to belong to a single species of dicynodont. This species is represented by the remains of at least eighteen individuals, as there are eighteen right distal ends of humeri; however, it is almost certain that there was really a somewhat greater number of individuals, all of which are only incompletely represented. These individuals come from a fairly restricted size range; in the humeri, for example, the proximal ends are from 8·5 to 10·0 cm. across and the distal ends are from 7·8 to 11·0 cm. across.

In addition to these individuals, there are the remains of a single individual of considerably larger size, the distal end of whose humerus is 17 cm. across. This specimen could be regarded either as a larger member of the same species as the numerous smaller individuals, or as belonging to a different, larger species.

There are several reasons for believing that the many smaller individuals are immature forms, and that the single large individual represents the adult of the same species. The immaturity of the small specimens is indicated by the lack of co-ossification and sutural union of the skull bones (even the bones of the braincase have not become firmly united) and by the poorly defined nature of the articular surfaces of the limb bones. On the humerus, for example, the articular areas for the glenoid, radius and ulna are hardly defined at all, while the articular surfaces of the radius, tibia and fibula are almost featureless and give the impression of having been covered in life with a thick capping of cartilage. Such surfaces on this and other bones have a characteristic appearance: the surface is smooth but interrupted by a large number of tiny round holes, the edges of which are often slightly raised, giving the appearance of tiny volcanic craters. In living reptiles this appearance is characteristic of surfaces covered by cartilage, and it will be referred to as " cartilage ornament " in the descriptive sections below.

The bones of the larger individual, on the other hand, have very well developed articular areas, but are otherwise identical with those of the smaller individuals. It is therefore regarded as the adult of the species, but is described separately, after the smaller individuals have been described, so as to facilitate any taxonomic change in its status, should this subsequently be found necessary.

A death-assemblage composed of a single adult and many juveniles is rather unusual. The flood which deposited the accompanying coarse grit may provide a possible explanation; it is conceivable that such a flood might cause a heavy mortality in the young dicynodonts, but that only a few of the larger adults would be caught and overwhelmed. The adult might even be a carcass of an individual which had died recently and which was caught up by the flood waters.

Zambiasaurus submersus sp. nov.

Text-figs. 1–20

The specific name *submersus* refers to the likelihood that the specimens were drowned.

Holotype of *Z. submersus:* Livingstone Museum (Zambia) specimen No. LM/NH 9/2, consisting of interparietal, left parietal and part of left squamosal of presumed immature individual.

Paratypes: British Museum (Natural History) catalogue Nos. R.9001–R.9140; Livingstone Museum (Zambia) specimen Nos. LM/NH 9/3–9/35.

Horizon and locality: Upper fossiliferous horizon of Triassic Ntawere Formation; from locality 15 of Drysdall & Kitching (1963), about 3½ miles west of Sitwe, in the upper Luangwa Valley, Eastern Province, Republic of Zambia (Field No. 15 A/1).

Description. As explained below the original skull morphology has had to be reconstructed and deduced from the eighty-five fragments listed above.

The most extensive fragment, which has been designated as the type specimen (Livingstone Museum specimen no. LM/NH 9/2; cast in B.M.(N.H.) is R.9000) comprises an interparietal, left parietal and part of the left squamosal (Text-fig. 1, b–e). The right parietal has become detached and lost, so that the sutural surfaces by which it was attached to the interparietal and left parietal are visible. It can therefore been seen (Text-fig. 1d) that the interparietal does not extend far forwards between the two parietals. The interparietal also does not extend far laterally before it joins the squamosal, neither does it overlap the occipital surface of the squamosal to any great extent. Though there is a sharp transition between the dorsal surface of the intertemporal bar and the posterior surface of the interparietal, there is also a recessed area in the dorso-median region of the interparietal, where the nuchal ligaments were presumably attached. Below this recess lies the occipital surface of the interparietal, in which there is a pair of nutrient foramina.

The dorsal surface of the left parietal is smooth and slightly concave antero-posteriorly. Though it is also slightly concave transversely, so that there would have been a very slight median ridge, the intertemporal bar as a whole is flattened, rather than forming an inverted V shape. The dorsal and lateral surfaces of the parietal meet at an acute angle (about 60°) and the lateral surface is shallowly concave dorso-ventrally. The posterior end of the lateral surface of the parietal is slightly damaged, but extended back to overlap the squamosal. The upper part of the lateral surface of the parietal is slightly recessed and bears the pitted and grooved ornament characteristic of a surface overlapped by another bone. There can be no doubt that this surface was covered by the posterior extension of the postorbital. Another specimen (R.9020) shows this surface even more plainly, and it is clear that the postorbital extended back as far as the junction between the parietal and the interparietal.

The parietal in the holotype forms the whole of the border of the left half of the pineal foramen (Text-fig. 1b). Another specimen (R.9020) in which this region is slightly better preserved, shows that the parietal forms a thin strip of the dorsal surface both lateral to, and anterior to, the pineal foramen (Text-fig. 1a). In neither specimen is there any trace of a suture delimiting a separate preparietal bone, and this bone must have been absent.

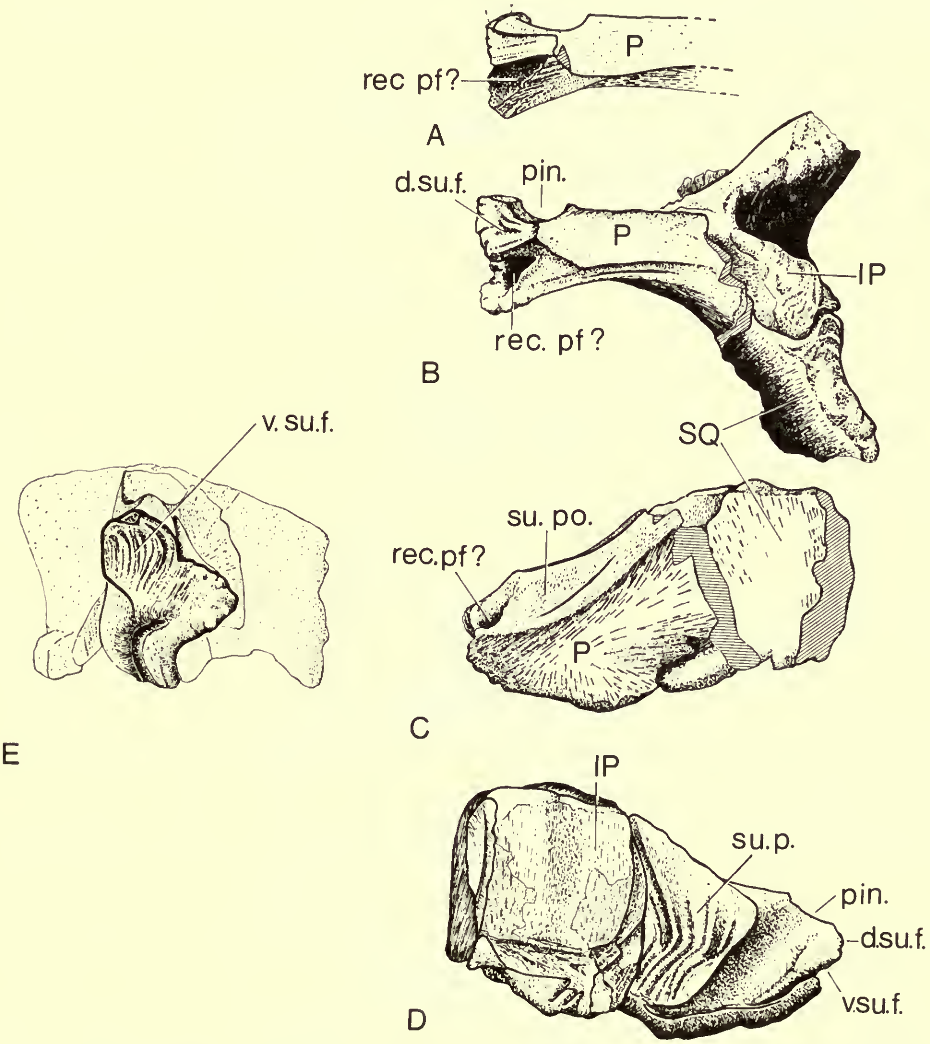

FIG. 1. *Zambiasaurus submersus* gen. et sp. nov., juvenile. × $\frac{2}{3}$. A, dorsal view of anterior end of left parietal, R.9020. B–E, holotype (Livingstone Museum No. LM/NH 9/2) in B, dorsal view; C, lateral view; D, medial view; E, anterior view. Abbreviations: d.su.f., dorsal sutural area for frontal; IP, interparietal; P, parietal; pin., pineal opening; rec.pf?, recess for ?postfrontal; SQ, squamosal; su.p., sutural area for right parietal; su.po., sutural area for postorbital; v.su.f., ventral sutural area for frontal.

Much of the anterior end of the dorsal surface of the parietal is covered by ridged, grooved and pitted areas of overlap (Text-fig. 1a, b). The most medial of these areas must have received the posterior end of the frontal (Text-fig. 1a, b) which therefore reached as far posteriorly as the level of the posterior border of the pineal foramen and also approached very close to its lateral and anterior borders (Text-figs. 1a, 2b, 20b). The most lateral area of sutural overlap on the antero-dorsal region of the parietal is that for the postorbital. Between this and the area for the frontal there is a deep posteriorly-directed recess (Text-fig. 1a–c: rec.pf ?). This

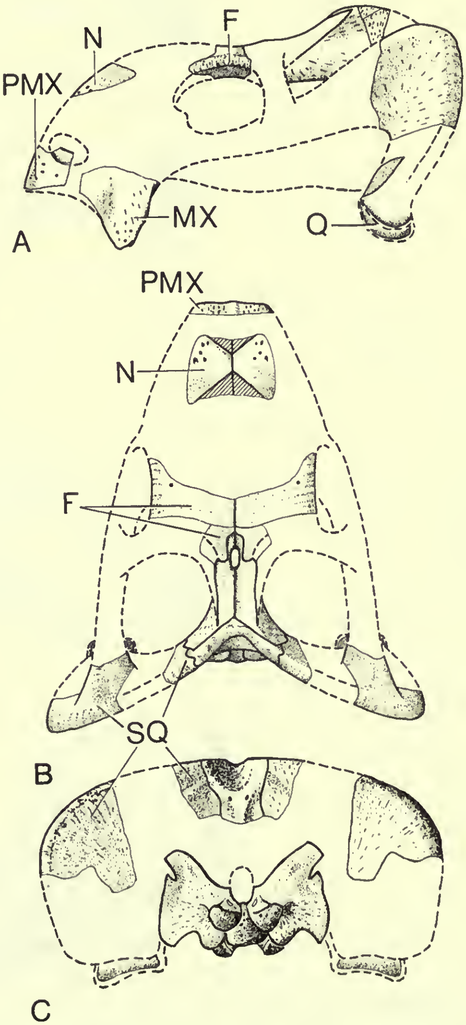

Fig. 2. *Zambiasaurus submersus* gen. et sp. nov. Drawings showing relationships of preserved fragments of skull to reconstruction of complete juvenile skull. × ¼. A, lateral view; B, dorsal view; C, occipital view. Abbreviations: F, frontal; N, nasal; MX, maxilla; PMX, premaxilla; Q, quadrate; SQ, squamosal.

recess may have received a small separate postfrontal bone. If it was present, this bone may have been concealed by a superficial meeting between the postorbital and the frontal.

There is a considerable angle between the more posterior part of the parietal and those areas to which the frontal attached. This fact, and the concave outline of the dorsal edge of the parietal in lateral view (Text-fig. 1c), suggests that the intertemporal bar projected postero-dorsally above the level of the rest of the dorsal surface of the skull (Text-fig. 2a). This is confirmed by fragment R.9014 (Text-fig. 3a), which comprises the region around the front end of the pineal foramen. The line of the dorsal edge of the intertemporal bar apparently continued forwards for a short distance on to that part of the frontal which lies antero-lateral to the pineal foramen, for this part of the bone is slightly thickened above the level of the rest of the frontal. This fragment also confirms that there is no preparietal bone and that the frontal overlaps the anterior end of the parietal. The frontal also extends posteriorly for a short distance under the parietal, where there is a wide sutural union between these two bones (Text-fig. 1d, e: v.su.f.).

The morphology of the area immediately in front of the pineal foramen, including the interorbital width, is shown by specimen R.9015. This is a large piece of a right frontal, including both the midline suture and part of the edge of the orbit. Specimen R.9016 is an almost identical fragment of a left frontal, on the postero-medial region of which can be seen the suture for attachment to the parietal. This fact is important, for it establishes the relationship between these frontal fragments, including the upper margin of the orbit, and the intertemporal bar. The resulting position of the orbit is relatively far back, so that the posterior edge of the post-orbital bar is at the level of the pineal foramen.

It is possible, but not certain, that the most antero-lateral corner of the frontal fragment R.9015 bears a short stretch of the surface to which the prefrontal bone was attached. Even if it does not, the suture cannot have been far anterior to this point, since that bone normally forms the antero-dorsal corner of the orbit.

Specimen R.9012 is part of a right nasal bone (Text-fig. 3b, c). The bone was overlapped postero-medially by the anterior end of the frontal, and antero-medially by the posterior end of the premaxilla. These surfaces are separated by only a short median sutural surface for the left nasal. In another, slightly larger, right nasal fragment (specimen R.9013) the overlap surfaces for the premaxilla and frontal meet, completely covering the median suture between the two nasals. The antero-lateral corner of these nasals bears a number of foramina.

The dorsal surface of the nasal R.9012 consists of two planes, which meet along a line which runs antero-laterally. The more postero-lateral plane faces dorso-laterally and represents the lateral surface of the snout. The anterior plane faces antero-dorsally and represents the beginning of the down-turning of the snout. This plane provides a clue as to the relative position of the nasal and of the anterior end of the snout since, together with the anterior surface of the premaxilla, it must form a smooth curve when seen in lateral view (Text-fig. 2a). Some hint as to the distance between the nasal and the anterior end of the premaxilla is also provided by the angle of the suture between these two bones, as seen along the front surface of the nasal. In most dicynodonts this suture runs to the antero-dorsal corner of the nostril in an almost straight line.

The front edge of the premaxilla is blunt, running transverse to the main axis of the skull. The grooves which lie lateral to the paired anterior palatal ridges therefore run on to the anterior edge of the premaxilla (specimen R.9001; Text-fig. 3d).

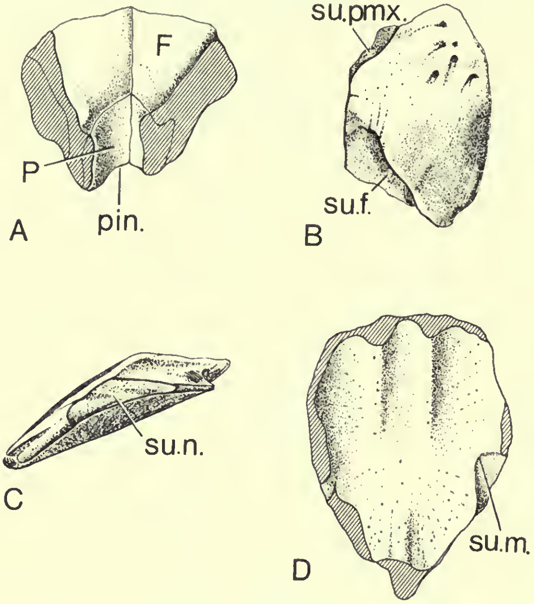

FIG. 3. *Zambiasaurus submersus* gen. et sp. nov., juvenile. × ⅔. Dorsal view of fragment R.9014 comprising area around anterior end of pineal foramen. B, C, fragment of right nasal (R.9012) in dorsal (B) and medial (C) views; D, ventral view of premaxilla (R.9001). Abbreviations: F, frontal; P, parietal; pin., pineal foramen; su.f., sutural area for frontal; su.m., sutural area for maxilla; su.n., sutural area for left nasal; su.pmx., sutural area for premaxilla.

There is little difficulty in fitting a maxilla (e.g. specimen R.9004) to the premaxilla. All nine maxillae are tuskless. Like the premaxilla and the anterior part of the nasal, the maxilla bears a number of nutrient foramina. There is a slight posteriorly directed flange down its postero-lateral edge.

At no point is there any junction between the preserved parts of the nasal-premaxilla-maxilla section and the more posterior section of the skull. It was therefore only possible to attempt to estimate the original relationship between these two sections by assembling each independently in a plasticene matrix and then matching them together, keeping the palatal surface of the premaxilla horizontal. The reconstruction shown appears quite plausible and does not violate any known normal feature of dicynodont morphology. Nevertheless, the exact distance between the two sections (and therefore the exact length of the frontal) must remain in doubt.

At the other end of the skull, there is similarly no certain relationship between the intertemporal-interparietal region and the remainder of the squamosal and braincase (Text-fig. 2). Most of the fragments of squamosal comprise the region where the zygomatic arch arises from the front surface of the occipital wing. The orientation of the base of the zygomatic arch, and also the orientation of the piece of squamosal attached to the interparietal of the type specimen (Text-fig. 1b) show that the squamosals extended laterally and somewhat posteriorly from the midline. The approximate width across the occiput follows from the interorbital width, since the zygomatic arches must have continued anteriorly and somewhat medially into the suborbital bar.

The fragments of braincase include a good basioccipital-basisphenoid (specimen R.9027) and a good exoccipital-opisthotic-prootic (specimen R.9028). The occipital condyle is of the normal tripartite dicynodont pattern. The tuber around the fenestra ovalis is formed partly by the basisphenoid and partly by the opisthotic. The opisthotic also forms the whole of the distal end of the paroccipital process; its anterior surface is covered by the prootic. Dorso-laterally, both the prootic and the opisthotic end abruptly in a thick surface, the ornament of which shows that it was capped by cartilage, and which presumably met the squamosal. The dorsal edge of the opisthotic, which slopes upwards and outwards, bears a similar ornament and must have joined the supraoccipital. The medial surface of the prootic and opisthotic bears the excavation for the inner ear.

The quadrate is of usual dicynodont type. Once again, its exact relationship to the remainder of the skull is uncertain, and it has merely been placed in the position normal in the group, at about the same level as the ventral margin of the premaxilla and ventro-lateral to the distal end of the paroccipital process.

Most of the fragments of lower jaw are of the articular region, which is of normal dicynodont type. Two fragments of the front end of the dentary (specimens R.9039, 9040) show that this was wide and blunt, as might have been expected from the shape of the premaxilla.

Postcranial morphology. To facilitate comparison, all bones are illustrated as viewed from the left side. Where necessary, bones from the right side have been reversed in the drawings so as to appear as left side bones.

There is a considerable number of fragmentary *vertebrae*. The prezygapophyses are usually concave, the postzygapophyses convex. The antero-dorsal corner of the lateral surface of the centrum bears a small facet for the lower end of the rib head. The remainder of the facet for the rib head extends postero-dorsally up the side of the neural arch. This facet extends to a varying degree up the ventral surface of the transverse process, which is dorso-laterally directed.

It is not possible to obtain any useful information from the fragments of *ribs*.

The *scapula* illustrated (Text-fig. 4) is reconstructed from two complementary fragments: a lower fragment (R.9068) and an upper fragment (R.9069). The blade is very long and narrow. There is a rather low scapular spine which runs for some distance up the antero-lateral edge of the bone (Text-fig. 4b) but which does not

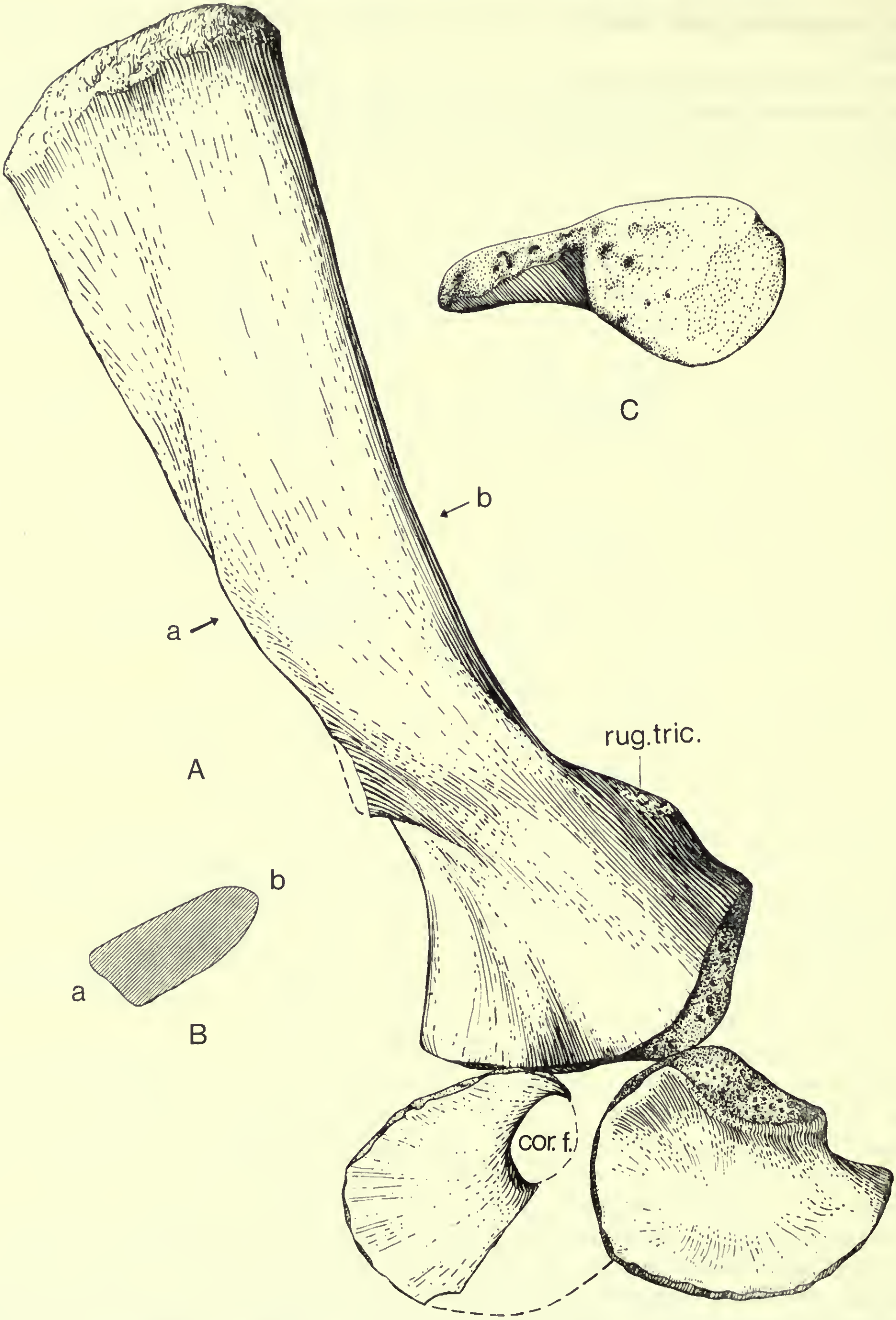

FIG. 4. *Zambiasaurus submersus* gen. et sp. nov., juvenile. Composite restoration. A, lateral view of scapula, precoracoid and coracoid (scapula and precoracoid are composite reconstructions); B, section through scapula at level a–b; C, view of ventral end of scapula, lateral surface uppermost. × $\frac{2}{3}$. Abbreviations: cor.f., coracoid foramen; rug. tric., rugosity for ligament of triceps muscle.

reach its upper end. The acromion process is damaged, but does not appear to have been very large. There is a pronounced rugose area on the postero-dorsal edge of the scapula a short distance above the glenoid; this is probably the area of origin of the scapular ligament of the triceps muscle. The glenoid surface is subcircular, but the surface for attachment of the precoracoid is quite thin (Text-fig. 4c).

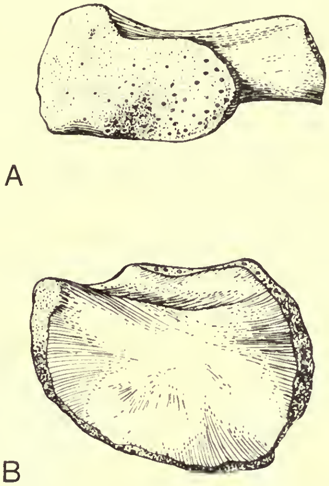

Fig. 5. *Zambiasaurus submersus* gen. et sp. nov., juvenile. Coracoid in A, dorsal view and B, medial view. $\times \frac{2}{3}$

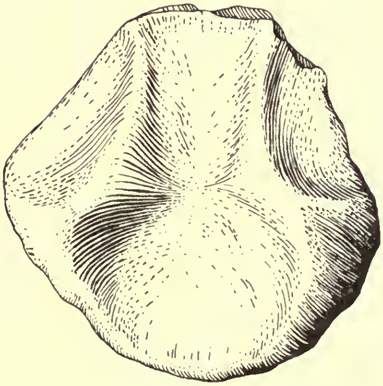

Fig. 6. *Zambiasaurus submersus* gen. et sp. nov., juvenile. Sternum in dorsal view. $\times \frac{2}{3}$.

The *coracoid* illustrated (specimen R.9073; Text-figs. 4, 5) is probably from a somewhat smaller individual than the scapula illustrated, as the scapular facet on the coracoid is narrower than the coracoid facet on the scapula. The outlines of these two surfaces do not, in any case, match; this is probably because there was still much cartilage between the elements of the girdles of these presumably juvenile individuals.

The *precoracoid* (Text-fig. 4) is incomplete; it is restored from three incomplete specimens (R.9078–80). Part of the edge of the coracoid foramen is preserved; since there is no notch in the lower edge of the scapula, this foramen must have lain wholly within the precoracoid.

Though a few fragments of *clavicle* are preserved, these give no useful information about the bone. No fragments of *interclavicle* have been identified.

The *sternum* (Text-fig. 6) is roughly hexagonal in outline. Its ventral surface is slightly concave. On its dorsal surface lie a pair of postero-lateral bosses, on the ends of which can be seen cartilage-ornament. These bosses probably gave insertion to the ventral ends of the anterior thoracic ribs.

Since no complete *humerus* is known, it has reconstructed mainly from two complementary fragments, a proximal fragment R.9088 and a distal fragment R.9089

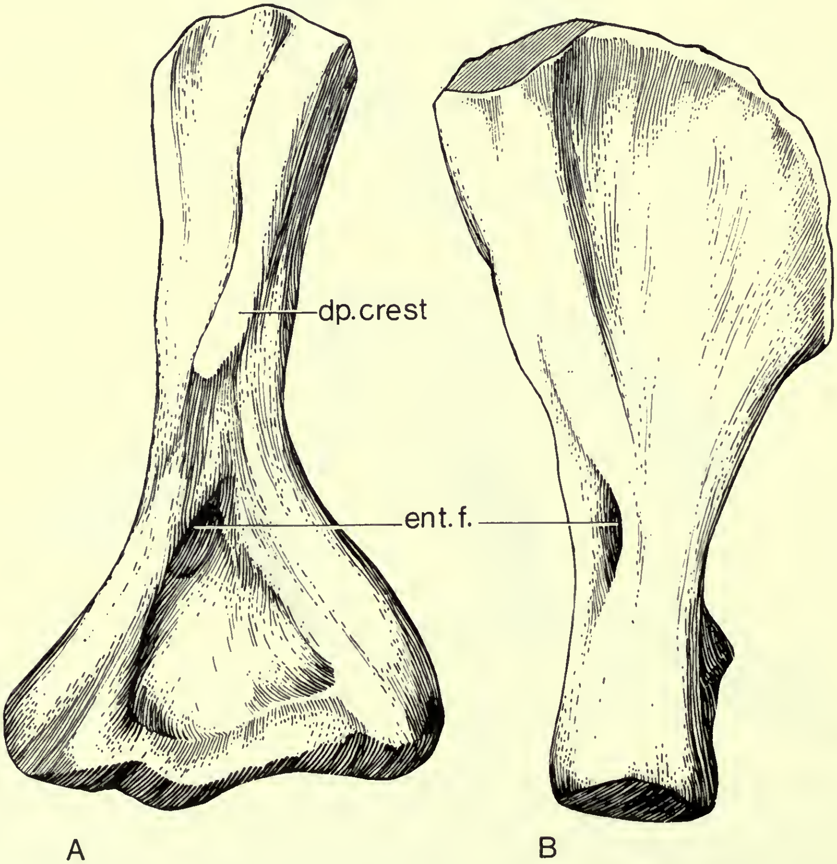

FIG. 7. *Zambiasaurus submersus* gen. et sp. nov., juvenile. Composite restoration of humerus in A, ventral view and B, posterior view. $\times \frac{2}{3}$. Abbreviations: dp.crest, deltopectoral crest; ent.f., entepicondylar foramen.

(Text-figs. 7, 8). It is strongly twisted. As in all the limb-bones, the areas of muscular insertion and of articulation are poorly defined, as might be expected in juvenile animals. There is thus little trace of the proximal condyle, nor of the condyles for the radius and ulna. Traces of cartilage-ornament can be seen over many of these surfaces, proving that the absence of the condyles is not due simply to erosion.

No complete *radius* is known, and the bone has been reconstructed (Text-fig. 9) from two proximal fragments (specimens R.9093, 9094) and two distal fragments (specimens R.9095, 9096). It is a slender bone and has been reconstructed to be, as is normal, slightly longer than the ulna. The proximal end is slightly convex, the distal end slightly concave.

A single complete right *ulna* is known (specimen R.9098, Text-fig. 9). The bone is fairly slender. Only the horizontal surface of the glenoid notch is represented. Since the whole of the proximal surface of the ulna is preserved (as proved by its covering of cartilage-ornament), the remainder of the sigmoid notch must have been

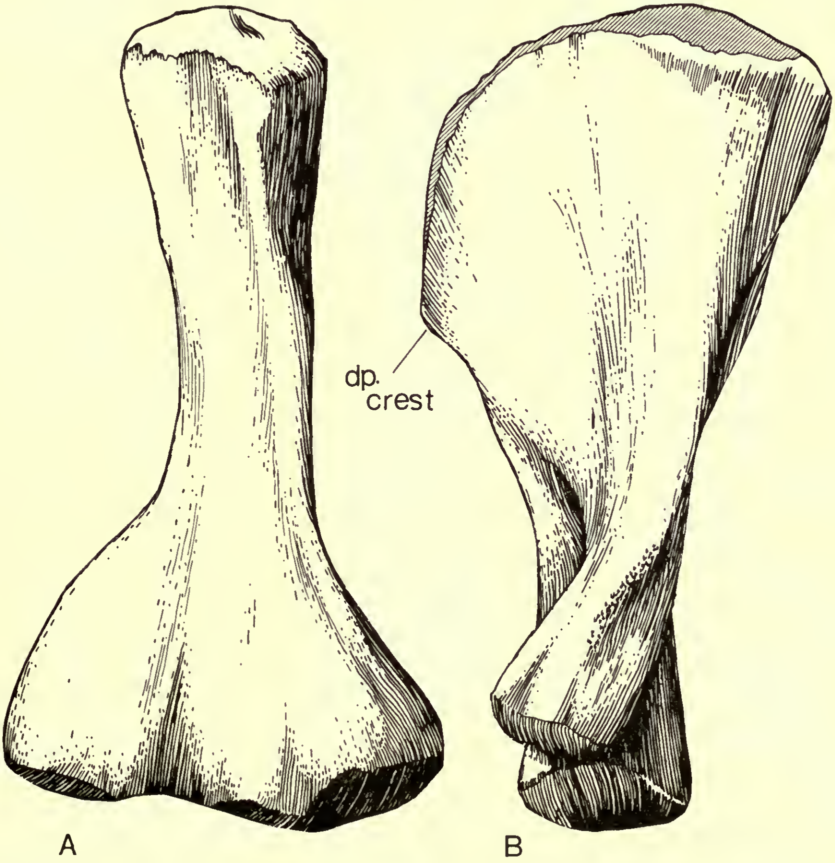

Fig. 8. *Zambiasaurus submersus* gen. et sp. nov., juvenile. Composite restoration of humerus in A, dorsal view and B, anterior view. × $\frac{2}{3}$. Abbreviations: dp.crest, delto-pectoral crest.

borne on a separately-ossified olecranon process. The distal end of the ulna is strongly convex.

Like those of the pectoral girdle, the bones of the pelvic girdle (Text-figs. 10–12) cannot be fitted together accurately, and much of the regions between the bones must still have been cartilaginous at this stage of growth.

The outline of the *ilium* has been based mainly on that of specimen R.9103, except for the extreme posterior preserved portion of the blade which is taken from specimen R.9106. The sacral facets are reconstructed from specimens R.9103–05.

The outer surface of the blade is slightly concave both dorso-ventrally and antero-posteriorly, while the inner surface is slightly convex in both these planes. The

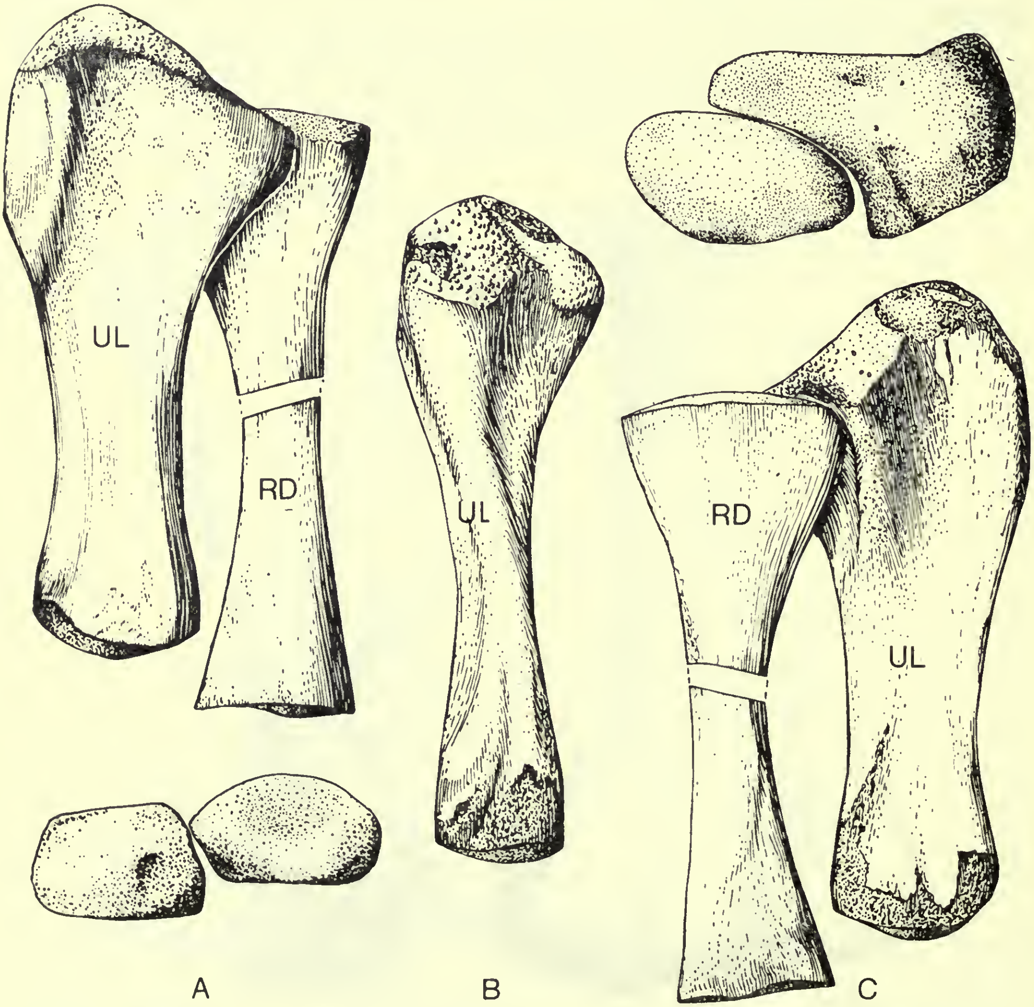

Fig. 9. *Zambiasaurus submersus* gen., et sp. nov., juvenile. A, radius (composite restoration) and ulna in posterior and distal views. B, medial view of ulna; C, radius (composite restoration) and ulna in anterior and proximal views. × $\frac{2}{3}$. Abbreviations: RD, radius; UL, ulna.

acetabular surface of the ilium faces ventro-laterally and slightly anteriorly. The facets for at least four sacral ribs can be distinguished on the inner surface of the blade (Text-fig. 12).

Most of the outline of the *ischium* (Text-figs. 10, 11) is based upon specimen R. 9108; most of the upper edge and a little of the posterior edge is complete. Specimen

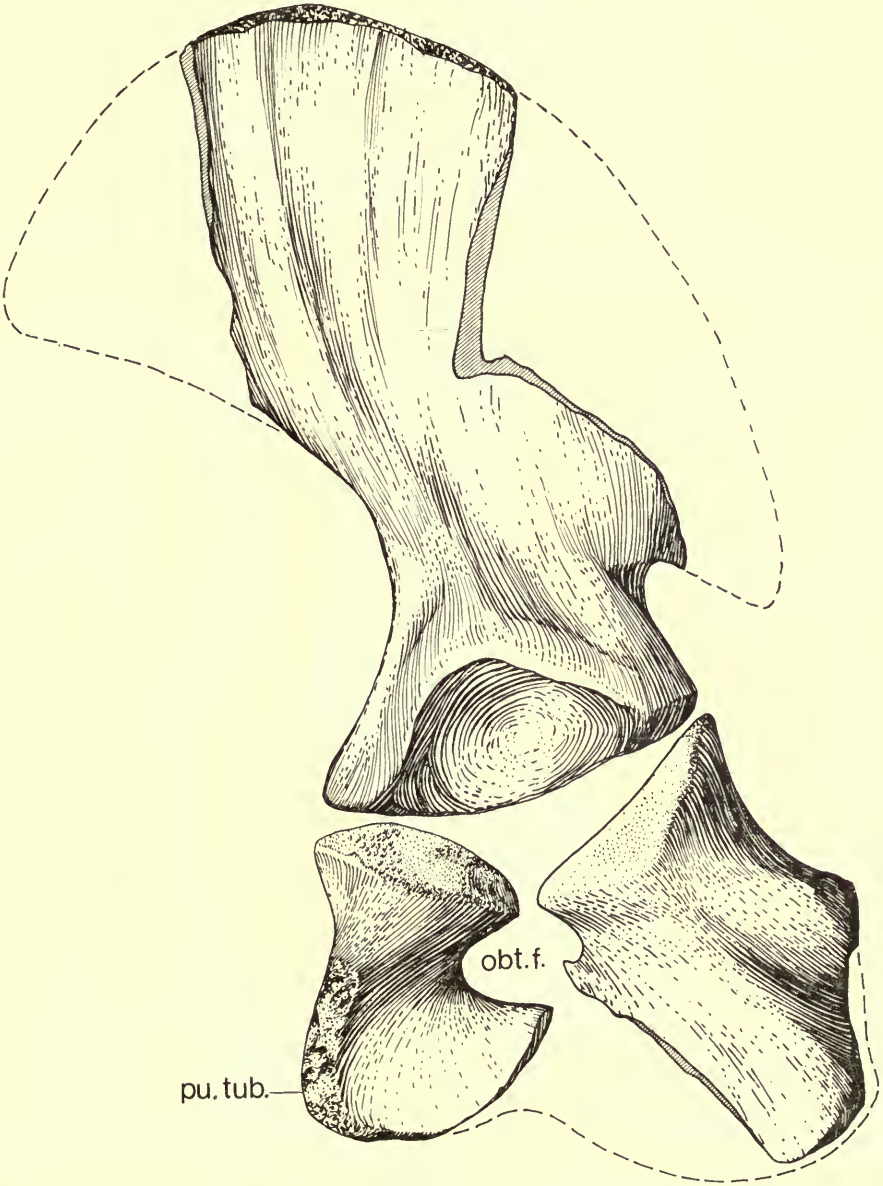

Fig. 10. *Zambiasaurus submersus* gen. et sp. nov., juvenile. Lateral view of pelvis. × ⅔. Abbreviations: obt.f., obturator foramen; pu.tub., pubic tubercle.

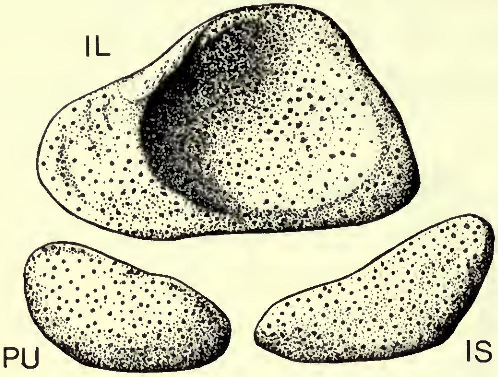

FIG. 11. *Zambiasaurus submersus* gen. et sp. nov., juvenile. Views of acetabular-articulatory surfaces of the ilium (IL), ischium (IS) and pubis (PU). × $\frac{2}{3}$. Lateral surfaces of the bones are peripheral, medial surfaces are central.

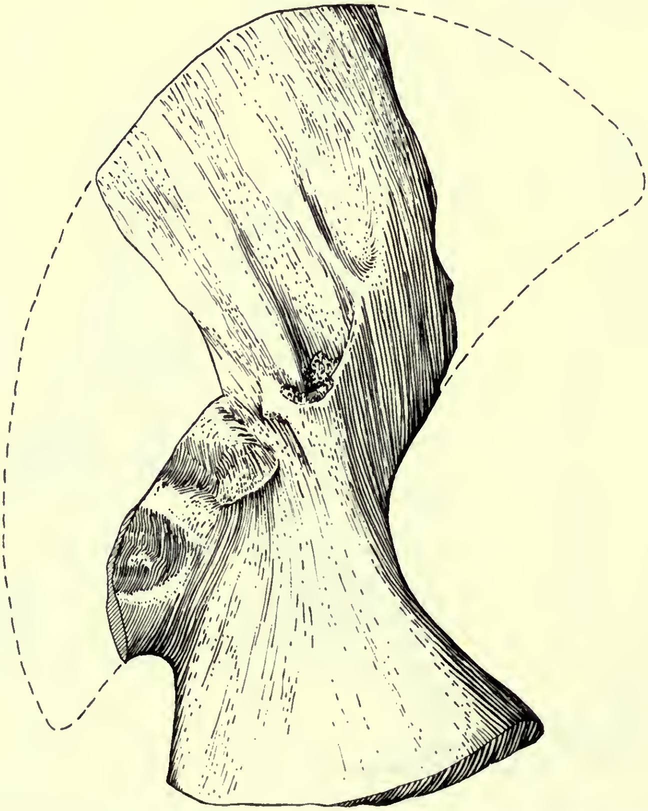

FIG. 12. *Zambiasaurus submersus* gen. et sp. nov., juvenile. Medial view of composite restoration of ilium. × $\frac{2}{3}$.

R.9109 includes a little more of the ventral portion of the bone. The anterior edge of the ischium is notched for the obturator foramen. The postero-dorsal region of the bone slants somewhat inwards, so that there is a stout ridge between this surface and the more antero-ventral region.

All edges of the *pubis* (specimen R.9113, Text-figs. 10, 11) bear cartilage-ornament, so that the figures show the bone complete at this stage of ossification. It bears a large convex face which must include the surfaces which articulated with the ilium and ischium, and also the pubic contribution to the acetabulum. Below this region the pubis projects antero-laterally to form a rather elongate pubic tubercle. The posterior edge of the bone is notched for the obturator foramen.

The *femur* illustrated (Text-fig. 13) is specimen R.9118, which is complete and from the right side; it is 18·5 cm. long. The articular facets are poorly developed. In side view it can be seen that the distal condyles were probably directed somewhat posterior to the main axis of the bone.

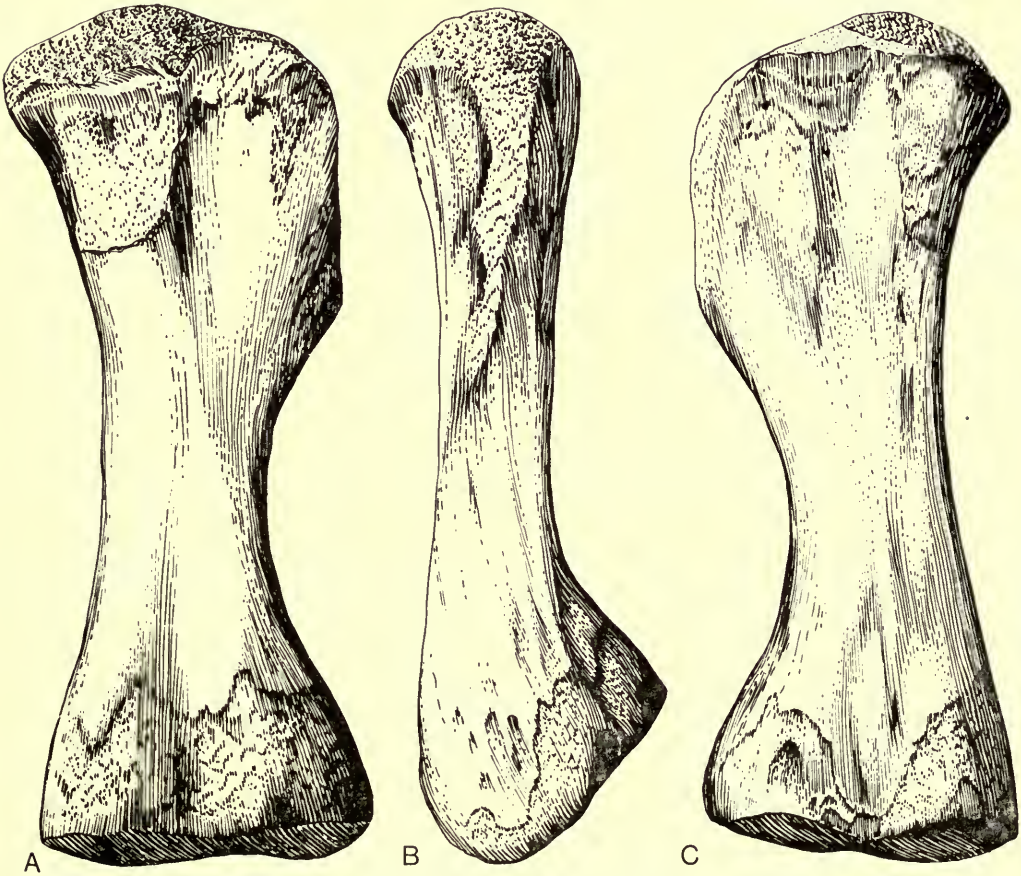

FIG. 13. *Zambiasaurus submersus* gen. et sp. nov., juvenile. Femur in A, anterior view; B, lateral view; C, posterior view. × $\frac{2}{3}$.

The *tibia* illustrated (Text-fig. 14) is specimen R.9123, which is also complete and from the right side. The proximal surface bears a pair of concavities for the femoral condyles. The lateral surface of this end of the bone is also slightly notched where it adjoined the proximal end of the fibula. The cnemial crest is represented by a thickening of the antero-lateral surface, which ends proximally in a surface which faces slightly anteriorly. The distal surface of the tibia can be divided into a moderately flat lateral region, and a markedly convex medial region.

The *fibula* is a slender, slightly curved bone (Text-fig. 14). The proximal end figured is specimen R.9128, while the distal end is specimen R.9129. The proximal end is convex; it is crescentic in outline, so that its medial edge curves around the lateral surface of the tibia. The distal articular surface is also convex, but is oval in outline.

Though a number of elements from the hand and foot are preserved, no useful information can be derived from them.

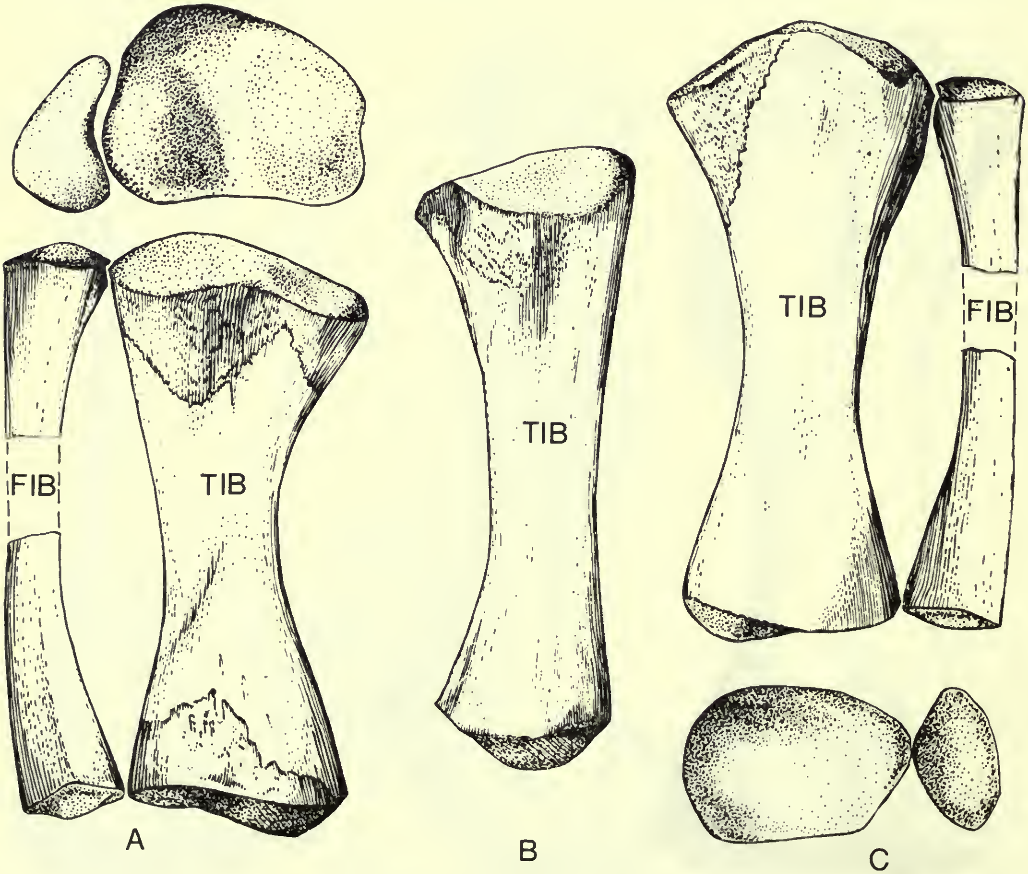

Fig. 14. *Zambiasaurus submersus* gen. et sp. nov., juvenile. A, tibia and fibula in posterior and proximal views; B, medial view of tibia; C, tibia and fibula in anterior and distal views. × ⅔. Abbreviations: FIB, fibula; TIB, tibia.

Adult specimen. Together with the remains of the immature specimens, there was preserved also a number of much larger dicynodont bones. Since no individual bone was duplicated, and since all of these bones were of commensurate size, it seems likely that all are derived from a single individual. They have therefore all been allocated a single specimen number, R.9140. They include a few uninformative fragments of skull and ribs, a few neural arches, two vertebral centra, a complete left coracoid and fragments of a pair of scapulae, a left humerus, a right radius, ulna and tibia, and a single phalanx.

One of the neural arches is almost complete, and is shown (Text-fig. 15) mounted upon one of the centra. The rib facet extends from the corner of the centrum up the side of the dorso-laterally directed transverse process, but does not reach its distal end. The outline of the dorsal end of the neural spine is restored from another specimen from this large individual. It is rather narrow antero-posteriorly, and slopes backwards at a considerable angle.

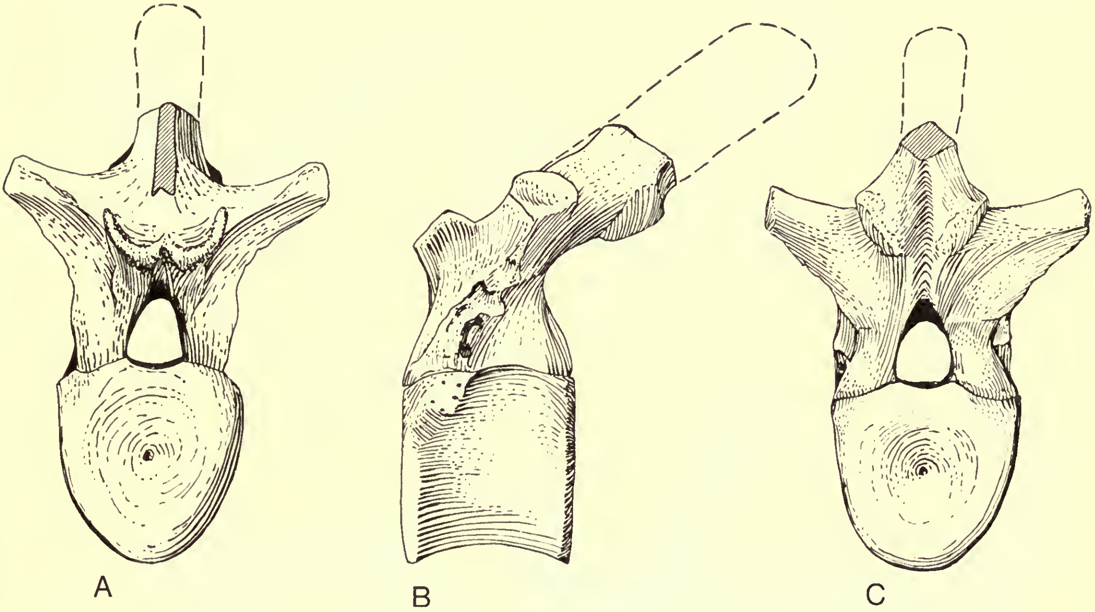

Fig. 15. *Zambiasaurus submersus* gen. et sp. nov., adult (R.9140). Neural arch and centrum (not originally associated) in A, anterior view; B, lateral view; C, posterior view. × ½.

The outline and morphology of the scapula (Text-fig. 16) and coracoid are identical to those of the immature specimen (cf. Text-fig. 4). In anterior or posterior view it can be seen that the blade of the scapula is curved to conform to the outline of the rib cage.

A fragment of the postero-dorsal corner of the proximal end of the humerus is preserved and shows a well developed articular condyle (Text-fig. 17a). The distal half of the bone (Text-fig. 17b, c) shows well developed condyles for the radius and ulna.

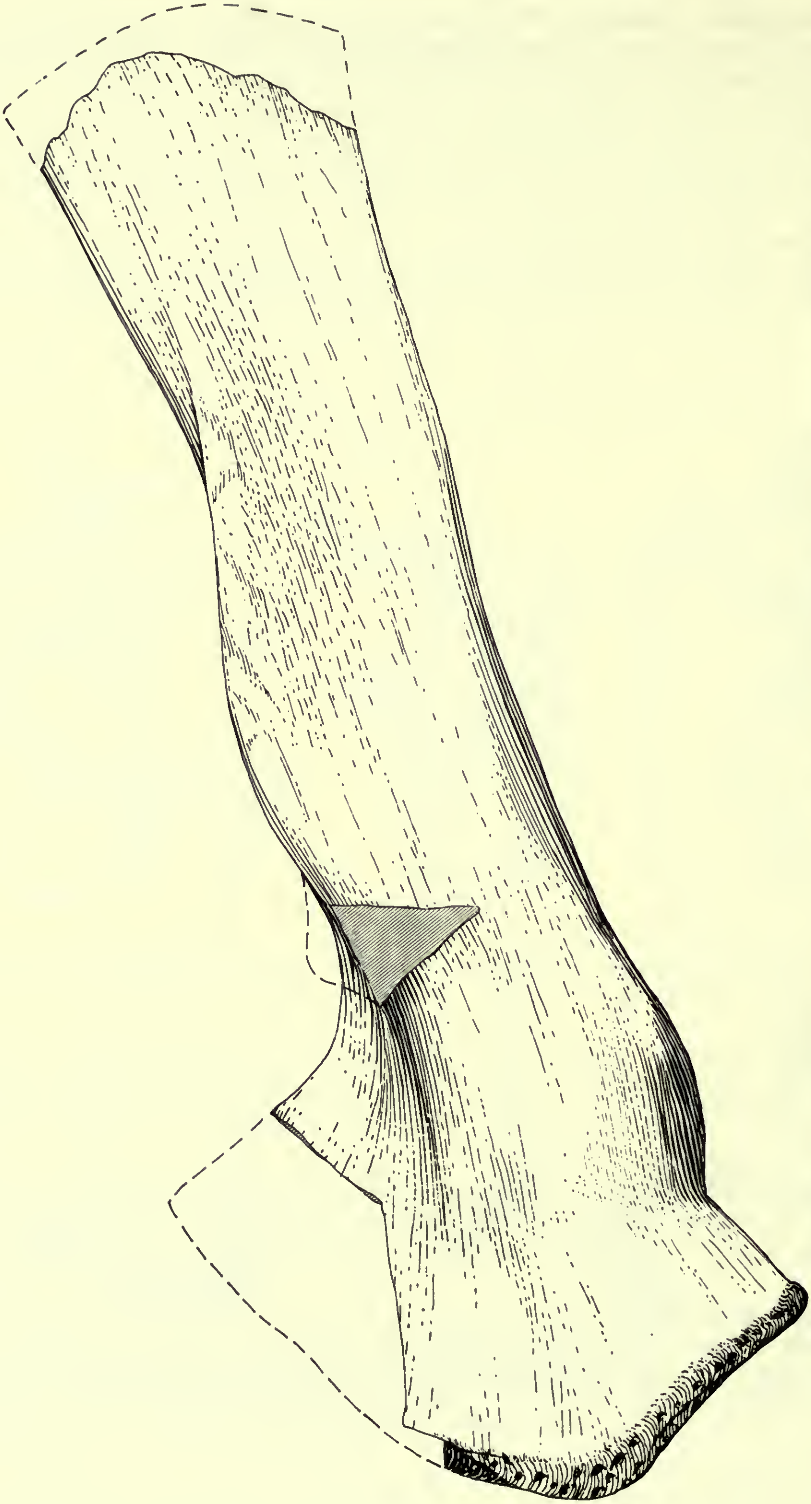

Fig. 16. *Zambiasaurus submersus* gen. et sp. nov., adult (R.9140). Lateral view of scapula, a little less than × ½.

The proximal ends of the radius and ulna, and the distal end of the ulna, are preserved. This fragment of radius shows no features of interest. The olecranon region of the ulna is lacking, and the proximal surface of the remainder of this end of the bone is unfortunately too poorly preserved for it to be possible to ascertain whether there was a separate olecranon ossification, as in other Triassic dicynodonts.

The proximal end of the tibia is well preserved (Text-figs. 18, 19). The pair of depressions for the femoral condyles are clearly visible. The cnemial ridge running up the antero-lateral face of the bone is better developed than in the immature specimen (cf. Text-fig. 14), and terminates in a rounded surface which is directed dorsally and anteriorly. A rugose area (Text-fig. 19, rug.) on the postero-lateral

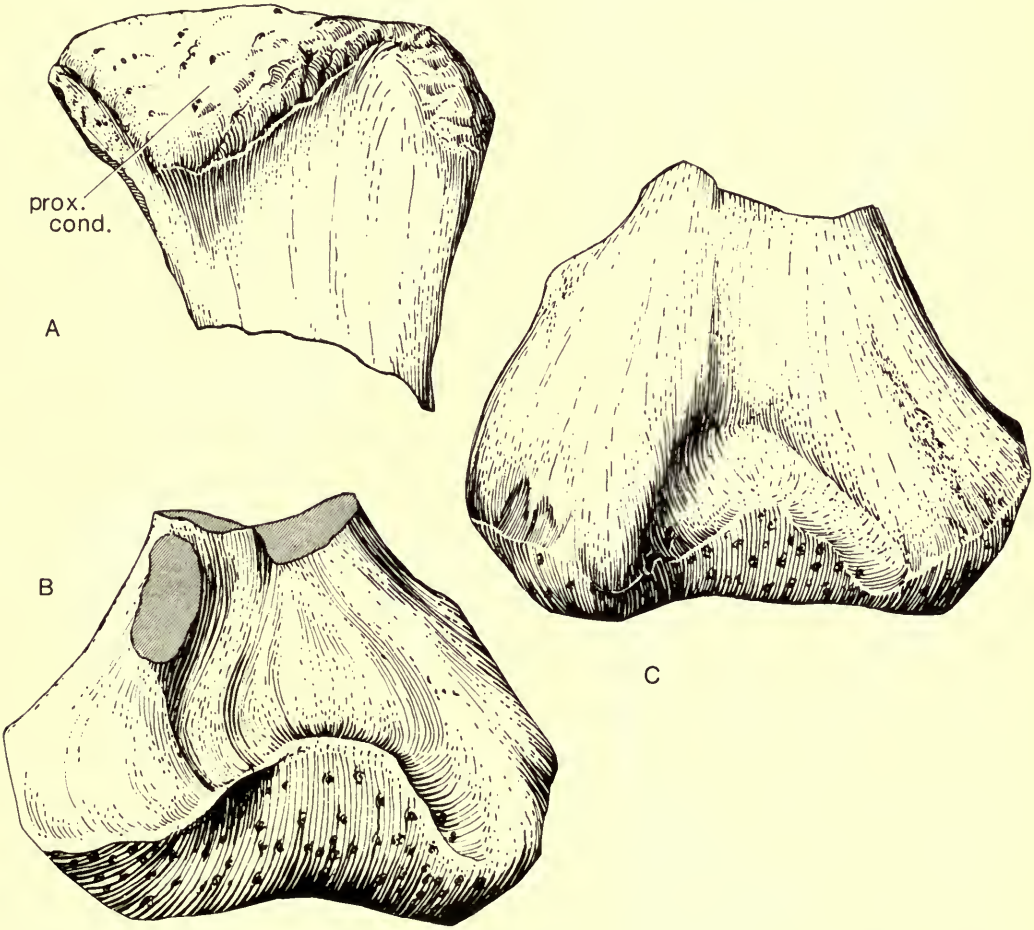

FIG. 17. *Zambiasaurus submersus* gen. et sp. nov., adult (R.9140). Humerus, × $\frac{2}{5}$. A, B, dorsal views of fragments (A) of proximal end and (B) of distal end; C, ventral view of fragment of distal end. Abbreviation: prox. cond., proximal condyle.

corner of the bone may mark the position where the proximal end of the fibula contacted the tibia.

If measurements (in cm.) of the bones of the adult are compared with those of the immature specimens figured, the following results are obtained.

	Juvenile	Adult	Adult/ Juvenile
Length of scapula	24	43	1·8
Length of coracoid	6·3	10·5	1·7
Width of distal end of humerus	9	17	1·9
Width of proximal end of radius	4·6	10	2·2
Width of proximal end of tibia	5·0	10·5	2·1

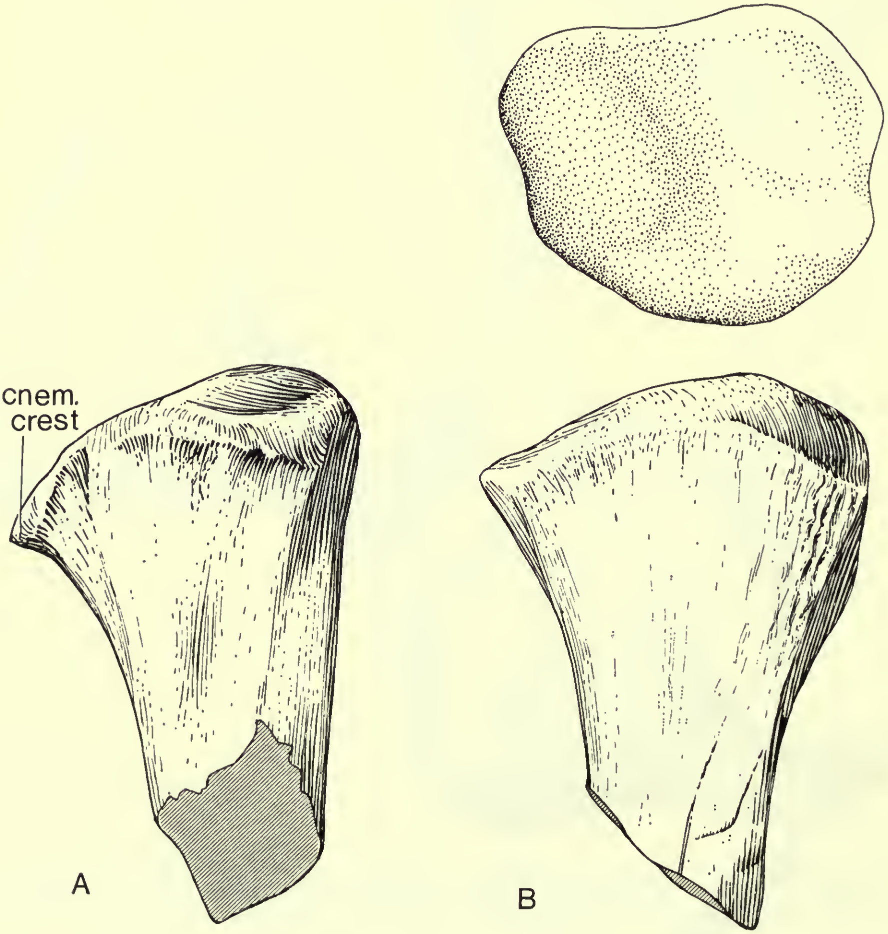

Fig. 18. *Zambiasaurus submersus* gen. et sp. nov., adult. (R.9140) Tibia. × ½. A, medial view; B, anterior and proximal views. Abbreviation: cnem. crest, cnemial crest.

It can be seen that the adult bones are about twice the size of the juvenile bones. If the skull of the adult was, similarly, about twice the size of the restored juvenile skull and retained a similar length : width ratio, it would have been about 45 cm. long and 40 cm. wide across the occiput.

DISCUSSION. *Taxonomy and relationships of Zambiasaurus.* There can, first of all, be little doubt that *Zambiasaurus* is a stahleckeriid, rather than a kannemeyeriid. Its blunt snout, wide but low occiput, short temporal opening and lack of a high intertemporal crest, are all similar to these diagnostic features of the family Stahleckeriidae as originally defined (Cox, 1965).

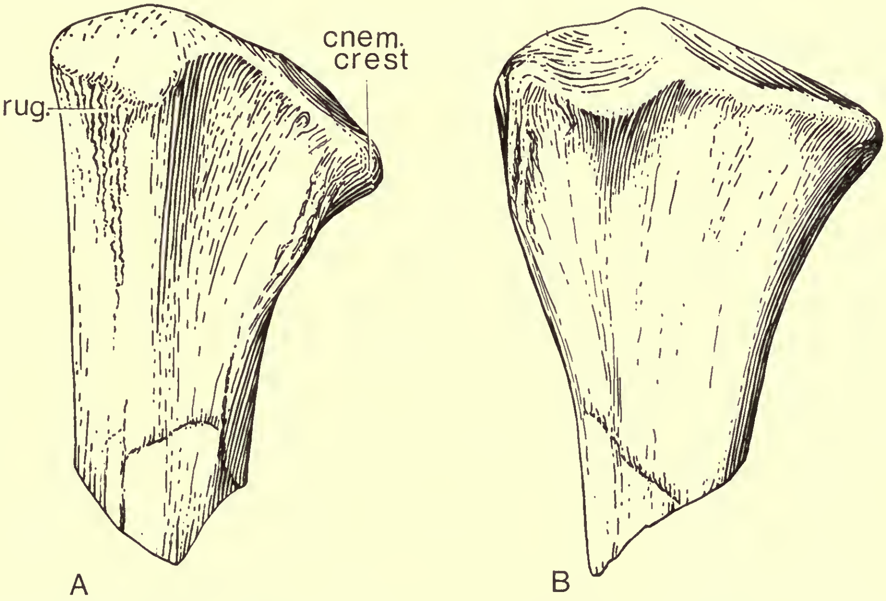

FIG. 19. *Zambiasaurus submersus* gen. et sp. nov., adult (R.9140). Tibia. × ½. A, lateral view; B, posterior view. Abreviation: cnem. crest, cnemial crest; rug., rugosity.

Zambiasaurus is the first stahleckeriid known outside South America. The Stahleckeriidae at present includes three genera: *Stahleckeria* of the Santa Maria Formation of Brazil, described by von Huene (1935–42); *Dinodontosaurus* from the above Brazilian Formation (Cox, 1965) and also from the Chañares Formation of Argentina (Cox, 1968) and *Chanaria*, also from the latter Formation (Cox, 1968). Both *Dinodontosaurus* and *Chanaria* have retained tusks and a preparietal bone, in contrast to *Stahleckeria* in which both these features are absent. Their absence in *Zambiasaurus* suggests that this new genus is more closely related to *Stahleckeria* than to the other two stahleckeriid genera.

Though tusks are frequently lost in dicynodonts, the absence of the preparietal is more rare. Comparison of the skulls of *Zambiasaurus* and *Stahleckeria* (Text-fig. 20) reveals several other similarities. Despite some superficial differences, the morphology of the whole intertemporal bar is very similar in the two genera. The parietals in *Zambiasaurus* can still be seen anterior to the pineal foramen, where they have occupied the space normally filled by the preparietal. In *Stahleckeria* the

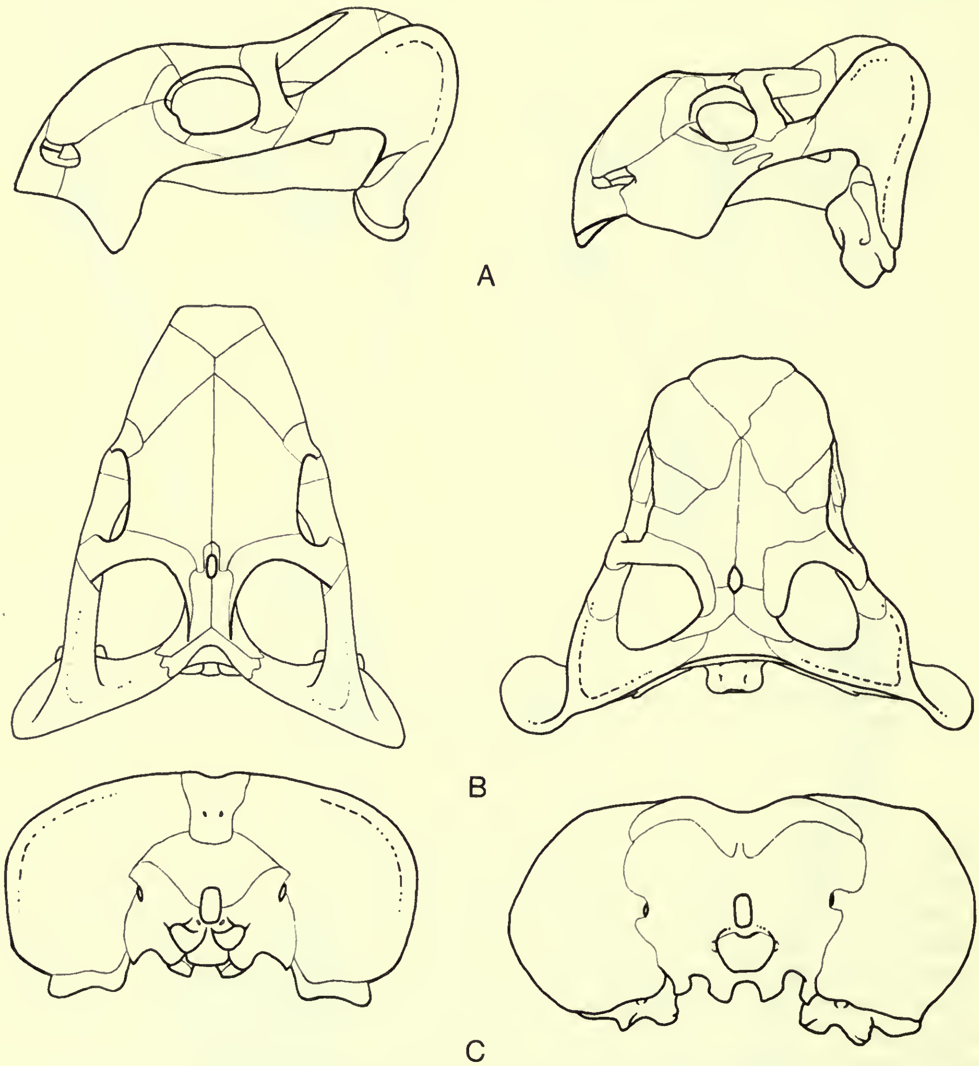

Fig. 20. *Zambiasaurus submersus* gen. et sp. nov., reconstructed juvenile skull × ¼ (left) and *Stahleckeria potens*, adult skull × *c.* 1/12 (right). A, lateral views: B, dorsal views; C, occipital views. (*Stahleckeria* after Camp, 1956).

frontals have extended slightly further back, enclosing the anterior half of the pineal foramen. In both genera the frontal meets the parietal at a level half way along the pineal foramen, the parietal forms a rather wide intertemporal bar which is almost flat in transverse section, and the interparietal contributes little to the intertemporal bar.

Another similarity between *Zambiasaurus* and *Stahleckeria* is that in both the nasals either meet for only a very short distance in the midline or are separated by a junction between the frontals and the premaxilla. In *Stahleckeria* this is probably a result of the very wide, massive snout; if the nasals lie far apart, the processes of ossification outwards from the centre of each bone might not reach the midline before this area had been ossified by the frontal. As far as one can tell, the snout of *Zambiasaurus* also was rather wide; this follows from the shape of the incomplete nasals, and the centre of ossification of the bone certainly lies more lateral than these fragments.

As far as the post-cranial skeleton is concerned, it is in any case difficult to find many systematic differences between the Triassic dicynodonts (see Cox, 1965 for a general survey). This difficulty is compounded in *Zambiasaurus* by the fact that most of the bones are known only in their juvenile state, with poorly developed processes for muscular insertion and articular condyles. A few similarities between *Zambiasaurus* and *Stahleckeria* can nevertheless be observed. The narrow, posteriorly-directed neural spine of *Zambiasaurus* (Text-fig. 15) is very like that of the anterior vertebrae of *Stahleckeria*. The coracoid, sternum and pelvis are in general similar in the two genera, there being a striking similarity between the ischium and pubis of *Zambiasaurus* and those of a juvenile *Stahleckeria* figured by von Huene (1935–42, Pl. 9, fig. 4). The difficulties mentioned above make it impossible to make useful comparisons between the limb bones of the two genera.

The absence of tusks, and of the preparietal bone, the morphology of the intertemporal bar and of the snout, and some post-cranial features thus all suggest that *Zambiasaurus* may be quite closely related to *Stahleckeria*. The Ntawere Formation, in which *Zambiasaurus* is found, is certainly older than the Santa Maria Formation, which contains *Stahleckeria*. It is therefore possible that *Zambiasaurus* may be actually ancestral to *Stahleckeria*, and the known differences between the two genera may now be examined with this possibility in mind.

As far as one can tell, the occipital wings of the squamosal are directed more posteriorly in *Zambiasaurus* than in *Stahleckeria*, so that its occiput is not as flat as that of *Stahleckeria*, and its temporal opening is slightly longer. The occiput itself, as restored, is not as wide in *Zambiasaurus* as in *Stahleckeria*. However, this feature could not, from the material preserved, be restored with any great degree of accuracy. It is also worth noting that the restored skull is that of a juvenile and that the occiput apparently does increase in relative size as the animal grows. This is suggested by the relatively larger occiput of the large specimen of *Dinodontosaurus turpior* which was described as a possible " old bull " (Cox, 1965, pp. 489–494).

Another difference between the occiputs of the two genera is that the interparietal of *Stahleckeria* may extend further laterally, as shown in Camp's (1956) reconstruction based on further study of von Huene's material. However, the outline of this bone is shown dotted in his figure (1956, Fig. 45) and this point is therefore uncertain. In any case, there is no obvious reason why the interparietal should not become wider during the evolution of the very wide occiput of *Stahleckeria*.

The snout of the " old bull " *Dinodontosaurus* mentioned above is also more massive than that of the smaller specimens, and this should be borne in mind when comparing the immature skull of *Zambiasaurus* with the adult skull of *Stahleckeria*, as these show a similar difference. The snout of *Stahleckeria* is extremely heavy and short, so that the centre of the maxilla lies under the anterior edge of the orbit. As reconstructed, the maxilla of *Zambiasaurus* lies further forwards. However, the exact inter-relationship between its maxilla and orbit cannot be determined from the fragments available (cf. Text-fig. 2) and, in any case, the condition shown in *Zambiasaurus* could well be ancestral to that found in *Stahleckeria*.

The interorbital region of *Stahleckeria* also differs somewhat from that of *Zambiasaurus* in that its nasal and prefrontal extend further posteriorly, so that the anterior half of the upper margin of the orbit is formed by the prefrontal instead of by the frontal as in *Zambiasaurus*. This, too, may be a result of the shorter snout of *Stahleckeria*, since the centres of ossification of the bones of this region must lie further posteriorly, so that they will encroach on the area formerly occupied by the frontal.

The only obvious difference between the post-cranial skeletons of *Zambiasaurus* and *Stahleckeria* is the shape of the scapula. In *Stahleckeria* (von Huene, 1935–42, Pl. 7, figs. 1–3) the scapula narrows above the glenoid region, but further dorsally it becomes progressively wider; there is a strong, antero-laterally directed acromion process, from which a stout spine runs up the outer surface of the blade near its anterior edge. In *Zambiasaurus*, on the other hand, the scapula does not expand dorsally, probably had a small anteriorly directed acromion process, and has a very low spine. However, there is no reason to suppose that the above features of the scapula of *Stahleckeria* could not have evolved from the condition found in *Zambiasaurus*.

To summarize, none of the known differences between the two genera precludes the possibility that *Zambiasaurus* is not only closely related to *Stahleckeria*, but is also directly ancestral to it. It is impossible, on the basis of present material, to test this hypothesis further; such tests will depend on the discovery of stahleckeriids of an age intermediate between that of the Ntawere Formation and that of the Santa Maria Formation.

Origin of the stahleckeriids. As will be shown later in this paper, the age of the Ntawere Formation may provisionally be estimated as lower Anisian. *Zambiasaurus* is therefore the oldest known stahleckeriid. As has already been shown, it is also probably ancestral to *Stahleckeria* and less closely related to the tusked genera *Dinodontosaurus* and *Chanaria*. The line leading to these tusked stahleckeriids must, then, have diverged from the tuskless *Zambiasaurus–Stahleckeria* line in or before the Lower Triassic (Scythian).

I have earlier (1965) suggested that the stahleckeriids (including all the above genera) may be separated from the kannemeyeriids on the basis of the form of the palate and occiput. The morphology of these areas is, of course, determined by the orientation and volume of the jaw muscles, and by the way in which the jaws are used during feeding. The modifications in the kannemeyeriid line (seen most clearly in *Kannemeyeria* and *Ischigualastia*) seem mainly to be directed towards increasing the antero-posterior length of the jaw muscles. This has been achieved by some exaggeration of that posterior extension of the squamosal which is common in Permian dicynodonts, and also by the postero-dorsal extension of the posterior region of the inter-temporal bar. These features seem to accompany a rather pointed premaxilla (e.g. *Sangusaurus*, see Text-fig. 22b) in which the anterior ends of the paired anterior palatal ridges of the premaxilla meet the converging lateral walls of the mouth cavity. As a result of this, the grooves which lie lateral to these ridges meet the antero-lateral margins of the snout, not its anterior edge.

The modifications of the stahleckeriids, instead, seem to have been directed towards an increase in the width of the skull and anterior end of the jaws. The posterior extension of the squamosal is lost altogether and the temporal opening is very short, but that part of the squamosal which lies lateral to the root of the zygomatic arch is greatly developed. This lateral development presumably provided attachment for muscles which would have allowed more accurate control of the lateral movements of the jaw than would have been possible in the kannemeyeriids. This may be correlated with the transversely widened anterior surface of both the premaxilla and the dentary. As a result of the width of this region, the paired palatal ridges of the premaxilla, and the grooves lateral to these ridges, run on to the anterior edge of the snout (Text-fig. 3d).

I have earlier (1965) suggested that these differences may be explained by their feeding habits, the kannemeyeriids having been browsers feeding on fronds and leafy branches, while the stahleckeriids were grazers, feeding on any low herb-cover similar to that provided by grasses today. Further understanding of the functional mechanical differences between these two groups will be possible only when well preserved undistorted skulls and jaws are available. These would permit the study of the sequences of possible jaw movements, in the same way as Crompton & Hotton's (1967) investigation of the functional morphology of two Permian dicynodonts, *Emydops* and *Lystrosaurus*.

It is at present impossible to suggest confidently any links between the Triassic dicynodont groups and the varied dicynodonts of the Upper Permian Kistecephalus Zone. Immediately above this zone lies the Lystrosaurus Zone, in which tiny *Myosaurus* and the aberrant lystrosaurids are the only dicynodonts known. Above this is the Cynognathus Zone from which *Kannemeyeria* is the only dicynodont described. Though the Sinokannemeyeria fauna of China is about the same age as the Cynognathus Zone fauna (though Bonaparte (1966) had tentatively suggested that the Sinokannemeyeria fauna might be younger than this, he no longer considers that this is likely [Bonaparte, personal communication]), the possible kannemeyeriids *Sinokannemeyeria* and *Parakannemeyeria* are very specialized in their long snouts, as Bonaparte (1966) has pointed out, a modification quite unlike the general trend in dicynodont evolution.

As a result of these facts, little can be said of the history of the stahleckeriids and the kannemeyeriids during the Scythian or (if their differentiation had taken place even earlier) during the late Permian. Dicynodonts with both the high, narrow type of skull (e.g. *Daptocephalus, Dinanomodon*) and the low, wide type of skull (e.g. *Aulacephalodon*) are found in the Upper Permian Kistecephalus Zone fauna of South Africa. There may or may not be phyletic connections between these Permian forms and the corresponding Triassic groups; it is, at present, impossible to decide.

Genus ***SANGUSAURUS*** nov.

DIAGNOSIS. Large dicynodont: complete skull would probably have been 35–40 cm. long. No teeth in upper or lower jaws. Premaxilla tapers anteriorly to blunt point. Median region of intertemporal bar markedly concave in transverse section. Low boss immediately posterior to pineal foramen. Interparietal forms posterior end of intertemporal bar.

TYPE SPECIES. *Sangusaurus edentatus* sp. nov.

Sangusaurus edentatus sp. nov.

Text-figs. 21–23

HOLOTYPE. Livingstone Museum (Zambia) specimen No. LM/NH 9/1 (Field No. 15 H/4) consisting of the following damaged bones: premaxilla, right and left maxillae, right and left quadrates; postero-dorsal corners of both squamosals; right prefrontal; intertemporal bar, consisting of interparietal and right and left parietals.

HORIZON AND LOCALITY. Upper fossiliferous horizon of Triassic Ntawere Formation; from locality 15 of Drysdall & Kitching (1963), about 3½ miles west of Sitwe, in the upper Luangwa Valley, Eastern Province, Republic of Zambia.

DESCRIPTION. The material was collected as isolated fragments over an area of about 50 square yards but, since all the bones are of commensurate size and no individual element is duplicated, it seems very likely that all belong to a single skull. Though much of this skull was not recovered, the fragments preserved are sufficient to demonstrate that it belongs to a new genus of dicynodont. The generic name *Sangusaurus* is derived from that of a nearby stream, the Sangu, while the specific name *edentatus* refers to the lack of tusks.

The most characteristic feature of the new genus is the intertemporal bar (Text-fig. 21). The median region of the parietals is quite deeply concave in section, as can be seen in posterior view (Text-fig. 21c). The sides of this trough form ridges, parts of the lateral surfaces of which may have been originally covered by the postorbitals, though the bone is too badly damaged for the areas of overlap to be distinguishable.

There is a low, median rugose boss immediately behind the pineal foramen. The anterior ends of the parietals are damaged, but what remains of these surfaces bears a pattern of vertical grooves similar to those found at the anterior end of the parietal of *Zambiasaurus* (cf. Text-fig. 1e). This suggests that these surfaces are those to which the frontals and preparietal were sutured.

The interparietal forms a wide contribution to the posterior end of the intertemporal bar and has a W-shaped suture with the parietals. There is an abrupt transition between this region of the interparietal and its occipital region (Text-fig. 21b, occ. surf. ip), since these two regions lie at a very acute angle (*c.* 25°) to one another. As preserved, the occipital surface of the interparietal therefore slopes very sharply antero-ventrally, and it seems unlikely that this is due to crushing, since this region of the skull is extremely solid. If it is undistorted, this orientation of the occipital surface of the interparietal implies that the whole intertemporal

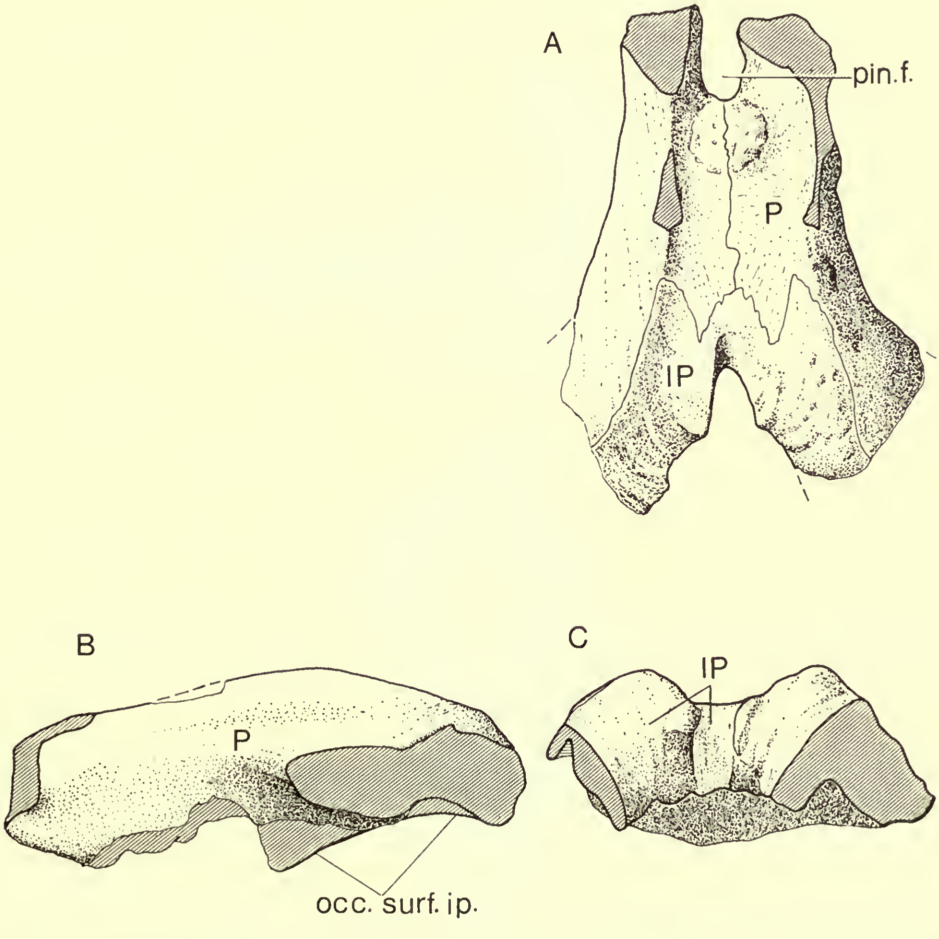

FIG. 21. *Sangusaurus edentatus* gen. et sp. nov., intertemporal bar of type specimen. × ½. A, dorsal view; B, lateral view; C, posterior view. Abbreviations: IP, interparietal; occ.surf.ip., occipital surface of interparietal; P, parietal; pin.f., pineal foramen.

bar was directed postero-dorsally, so that its posterior end projected backwards above the occiput.

The palatal surface of the premaxilla (Text-fig. 22b) bears a pair of anterior palatal ridges. The premaxilla tapers anteriorly, so that the anterior ends of these ridges meet the converging lateral surfaces of the bone. The grooves lateral to these ridges therefore do not emerge along the anterior edge of the premaxilla, but along its antero-lateral edges, and they are more shallow than the median groove which lies between the palatal ridges. The outer surface of the anterior end of the premaxilla bears a median ridge and a pair of lateral ridges.

The right maxilla (Text-fig. 3) is more complete than the left. There is no sign of a tusk either in the caniniform processes or in either maxillary antrum. A fairly well developed flange runs down the postero-lateral edge of the bone. The

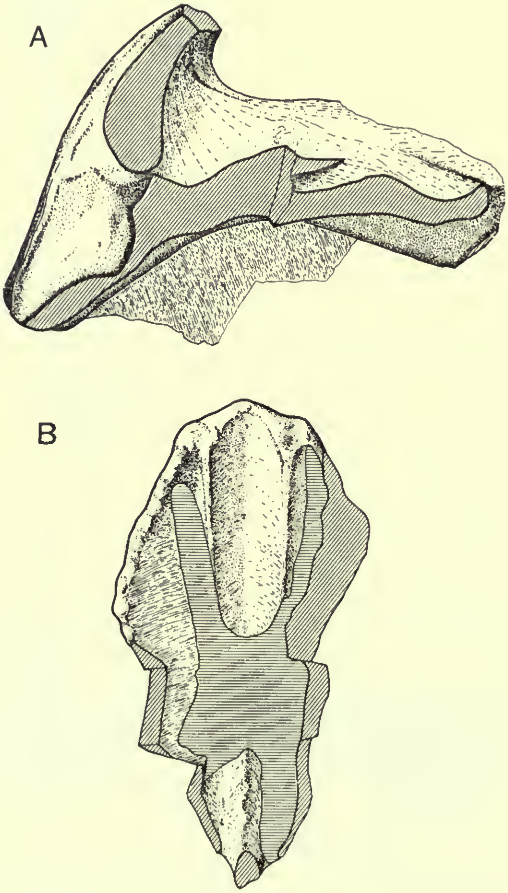

Fig. 22. *Sangusaurus edentatus* gen. et. sp. nov., premaxilla of holotype. × ½. A. lateral view; B, ventral view.

palatal surface of the maxilla is slightly recessed anteriorly where it would have been overlapped by the premaxilla. If the maxilla is orientated so that its caniniform process is directed vertically, the ventral edge of this recess runs antero-ventrally at a considerable angle to the horizontal. However, the premaxilla-maxilla suture in this region in most dicynodonts runs approximately horizontally, parallel to the palatal surface. Such a result can be achieved only if the caniniform process is swung forwards so as to have a very marked antero-ventral orientation.

The isolated right prefrontal and a few other damaged and unidentifiable fragments show no features of significance.

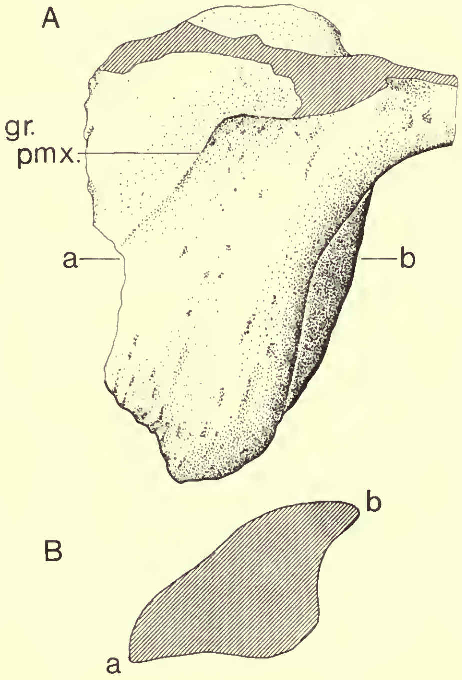

Fig. 23. *Sangusaurus edentatus* gen. et sp. nov., maxilla of holotype. × ½. A, lateral view; B, section through maxilla at a–b. Abbreviation: gr.pmx., groove marking lower limit of area of maxilla originally covered by premaxilla.

Discussion. *Taxonomy and relationships of Sangusaurus.* There can, first of all, be no doubt that *Sangusaurus* is generically distinct from all other dicynodonts, since the features mentioned in the diagnosis are not found together in any previously known genus.

Several features indicate that *Sangusaurus* is a kannemeyeriid rather than a stahleckeriid. These features include the postero-dorsally directed intertemporal bar (if the posture of this region has been interpreted correctly above) and anteriorly taping premaxilla, the palatal ridges of which meet the lateral edges of the bone, not the anterior edge. The well developed flange down the posterior surface of the maxilla is also commonly found in kannemeyeriids (though a small flange is present in the stahleckeriid *Zambiasaurus*).

The Kannemeyeriidae at present includes six genera: *Kannemeyeria*, from the Lower Triassic Cynognathus Zone of South Africa, the Middle Triassic Manda Formation of East Africa, and the Middle(?) Triassic Puesto Viejo Formation of Argentina (Bonaparte, 1966, 1967); *Sinokannemeyeria* and *Parakannemeyeria*, both from the Lower Triassic Er-ma-ying Formation of Shansi, China; *Barysoma*, from the Middle Triassic Santa Maria Formation of Brazil; *Ischigualastia*, from the Middle or Upper Triassic Ischigualasto Formation of Argentina, and *Placerias* from the Upper Triassic Chinle Formation of Arizona, U.S.A. The morphology of *Ischigualastia* and *Placerias*, and the inter-relationships of all the above genera have been discussed in an earlier paper (Cox, 1965).

Compared with the above kannemeyeriids (except *Barysoma*, whose skull is known only from a partial occiput), the structure of the intertemporal bar of *Sangusaurus* is closest to that of *Ischigualastia*. In both genera the median region of the parietals is concave in transverse section, there is a W-shaped suture between the parietals and the interparietal, and the posterior end of the intertemporal bar (again, if correctly interpreted in *Sangusaurus*) projects posteriorly above the occiput. The intertemporal bars of the other genera differ. That of *Placerias* is much wider than that of *Sangusaurus* and is flatter dorsally in cross-section. That of *Kannemeyeria* is very narrow, forming a sharp median crest. Those of both *Sinokannemeyeria* and *Parakannemeyeria* are moderately wide and are concave dorsally, but are not postero-dorsally directed, and there is therefore a more gradual transition from the dorsal surface of the intertemporal bar on to the occiput.

Though similar to one another in general, the intertemporal bars of *Sangusaurus* and *Ischigualastia* differ in that the interparietal is much longer in *Ischigualastia* and forms the whole width of the posterior end of the intertemporal bar, and the dorsal surface of its interparietal is convex, not concave as in *Sangusaurus*.

Another similarity between *Sangusaurus* and *Ischigualastia* is the lack of tusks in both genera. All the remaining kannemeyeriids are tusked. (This region is unknown in *Barysoma*, which appears to be closely related to *Ischigualastia*.) However, this similarity is less significant than the similarities noted above, as many dicynodont genera have lost the tusks. If the antero-ventral orientation of the caniniform process of *Sangusaurus* suggested above is correct, this is another feature known only in this genus and in *Ischigualastia*.

The above comparisons suggest that *Sangusaurus* is more closely related to *Ischigualastia* than to the other known Triassic kannemeyeriids. However, *Sangusaurus* is so incompletely known that it would be unwise to place too much reliance upon these resemblances, or to regard a relationship between the two genera as definitely established.

IV. AGE OF THE NTAWERE FAUNAS

Before the significance of the faunas of the Ntawere Formation can be appreciated, it is first necessary to establish the Triassic faunal sequence into which they must be inserted. I shall therefore first discuss the faunas and ages of three other units: the Cynognathus Zone of South Africa, the Molteno Beds of South Africa and the Manda Formation of Tanganyika (Tanzania).

1. *Cynognathus Zone.* This is the uppermost unit of the Beaufort Series. The fauna includes cynognathid, diademodont and trirachodont cynodonts, the very primitive rhynchosaurs *Howesia* and *Mesosuchus*, and the primitive pseudosuchians *Euparkeria* and *Erythrosuchus*. The only dicynodont which has been described is *Kannemeyeria*; however, two other undescribed genera are known, one in the collection of the Bloemfontein Museum, South Africa, and the other in that of the Smithsonian Institution, Washington. Though the Cynognathus Zone is up to 2,000 feet thick, this fauna is found only in the lowest 500–600 feet (Hotton & Kitching, 1963).

I have recently (Cox, 1967) suggested that the Cynognathus Zone may be best regarded as of Upper Scythian age. This estimate was based upon the presence in the underlying Lystrosaurus Zone (itself regarded as Lower Scythian in age) of the capitosaurid labyrinthodont *Wetlugosaurus*, which had also been identified from a bed in Greenland above a zone containing a dateable ammonite fauna. Though Welles & Cosgriff (1965) have pointed out the unreliability of the Greenland specimens in particular, and of this " genus " in general, Cosgriff has also provided a better basis for the dating of the Cynognathus Zone. He has described (Cosgriff, 1965) a new Australian temnospondyl which is associated with microfloras and marine fossils, both of which indicate a Lower Scythian age. It is closely related to *Peltostega* of the Upper Scythian Poisdonomya Beds of Spitzbergen, and to *Rhytidosteus* of the Cynognathus Zone. Cosgriff (1965) also points out that comparison of the temnospondyl amphibians of the Cynognathus Zone with those of the Lystrosaurus Zone suggests that there was probably an appreciable time lapse between these two faunas. Relevant here is Hotton & Kitching's (1963) comment, based on geological interpretation, that the Cynognathus Zone may have been deposited after a considerable interval of erosion. All these facts may be reconciled and accommodated if the Lystrosaurus Zone is regarded as of Upper Permian age (as Cosgriff, 1965, suggests), and is followed by a gap in the record, equivalent to the Lower Scythian, which is in turn followed by the Upper Scythian fauna from the lower part of the Cynognathus Zone.

2. *Molteno Beds.* These beds were originally regarded as barren. Boonstra (1947) described a cynognathid cynodont, *Cynidiognathus longiceps*, collected by Stockley in what he thought were lower Molteno Beds of Basutoland (now Lesotho). This species is known from the Cynognathus Zone, and it is now thought possible that this specimen may have come from nearby exposures of that Zone. More recently, Crompton & Ellenberger (1957) described a traversodont cynodont, *Scalenodontoides*, from the upper Molteno Beds; however, Crompton (1968, personal communication) now considers that the level from which this specimen originated lies in the strata which are transitional between the Molteno Beds and the overlying Red Beds, not in the typical Molten Beds. As a result, once again, vertebrate fossils are unknown from the Molteno Beds. These beds, up to 1,900 feet thick, may therefore cover all or part of the time between the underlying Upper Scythian

Cynognathus Zone and the overlying Red Beds. These latter contain a varied dinosaur fauna, including melanorosaurs, thecodontosaurs and sauropod-like footprints, and are probably of Upper Triassic age (Charig, Attridge & Crompton, 1965). No more accurate assessment can at present be made than that the Molteno Beds therefore represent part or all of the Middle Triassic (Ladinian and Anisian).

3. *Manda Formation.* This fauna lacks the more primitive cynognathid and diademodont cynodonts found in the Cynognathus Zone, but instead includes traversodont cynodonts. Both the rhynchosaur and the diverse pseudosuchians are far more advanced and common than are those of the Cynognathus Zone. The dicynodonts include a greater variety of forms than the Cynognathus Zone, but the genus *Kannemeyeria* is still present. The Manda fauna has provisionally been regarded as of Anisian (possibly Upper Anisian) age (Cox, 1965, 1967).

4. *Ntawere Formation.* As already mentioned, this formation contains two fossiliferous horizons, which will be discussed separately. That from the lower part of the formation contains two undescribed new tusked dicynodonts (in the collection of the Bernard Price Institute for Palaeontological Research, Johannesburg), the cynodont *Diademodon rhodesiensis*, and fragments of large labyrinthodonts. The age of this fauna must at present depend upon the characters of the cynodont. Brink (1963 : 79) states that this is " very typically a *Diademodon* and it is very difficult to find a particular feature about the skull on the strength of which it can emphatically be differentiated from a known species like *D. polyphagus* " (of the Cynognathus Zone). Brink notes, however, that the post-dentary bones are more reduced, and the coronoid process of the dentary better developed, than in the Cynognathus Zone species. These somewhat advanced features may indicate that this Ntawere fauna is slightly younger than that of the Cynognathus Zone, and it might conveniently be regarded as equivalent to the upper, non-fossiliferous, portion of the Cynognathus Zone.

The upper fossiliferous horizon extends over the topmost beds of the Ntawere Formation and the lower part of the Red Marl. Its fauna includes the stahleckeriid dicynodont *Zambiasaurus*, the kannemeyeriid dicynodont *Sangusaurus*, two traversodont cynodonts (*Luangwa drysdallensis* Brink 1963 and another specimen which will be described by Crompton), fragments of pseudosuchians, and the remains of the largest known labyrinthodont amphibian, approximately twice the size of *Paracyclotosaurus* (which will be described by Panchen).

The absence of diademodonts (as far as is known), the presence of traversodonts and its stratigraphical position above the lower fossiliferous horizon (itself of possible Cynognathus Zone affinities) all indicate that this upper Ntawere fauna is younger than the Cynognathus Zone. The above characters of its cynodont fauna similarly indicate a closer relationship to the Manda fauna. The only remaining problem is whether this Ntawere Fauna should be regarded as older than, or the same age as, the Manda Formation. The only fact relevant to this decision is the absence from the Ntawere fauna of the rhynchosaurs which form such a large element in the Manda fauna. Though, as has been pointed out previously (Cox, 1967), this group is notably unreliable as a faunal indicator, it must be accepted here in the absence of any more reliable evidence. The upper fossiliferous horizon of the Ntawere Formation is therefore provisionally to be regarded as slightly older than the Manda Formation. If this is so, the suggestion of Dixey (1936) and of Drysdall & Kitching (1964) that the Escarpment Grit (which underlies the Ntawere Formation) may be equivalent to the Kingori Sandstone (which underlies the Manda Formation) must be incorrect unless the Kingori Sandstone is equivalent to both the Ntawere Formation and the Escarpment Grit. It is, perhaps, more likely that the Kingori Sandstone represents a later phase in the sedimentary cycle which began with the Escarpment Grit.

TABLE I

	South Africa	Zambia	Tanzania
Rhaetian	Cave Sandstones		
Norian	Red Beds		
Carnian	Molteno Beds		
Ladinian			
U. Anisian			Manda Formation
L. Anisian	Unfossiliferous U. Cynognathus Zone	Ntawere Formation	Kingori Sandstone
U. Scythian	Cynognathus Zone fauna	Escarpment Grit	
L. Scythian			
U. Permian	Lystrosaurus Zone		
,,	Kistecephalus Zone	Madumabisa Mudstone	Kawinga Formation

V. ACKNOWLEDGMENTS

Most of the expenses of the 1963 expedition, during which these specimens were collected, were met by grants from the Department of Scientific and Industrial Research and the Royal Society; grants were also kindly made by the Percy Sladen Memorial Fund, the Godman Exploration Fund and Shell Research Ltd. All the members of the Expedition are grateful to these bodies for their support, which made the Expedition possible.

The drawings in this paper are by Miss J. Joffe and Mr. P. Hutchinson, who were in turn employed as my research assistant. The salary of this post was met from a special grant of the Natural Environment Research Council, for whose support I am greatly indebted.

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BRITISH MUSEUM 5 MAR 1969 NATURAL HISTORY

PRINTED IN GREAT BRITAIN
BY ADLARD & SON LIMITED
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NATURAL HISTORY

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Pp. 295–376; 18 *Plates*, 15 *Text-figures.*

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World List abbreviation :
Bull. Br. Mus. nat. Hist. (Geol.).

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Issued 15 *April,* 1969 *Price* £4 15*s*.

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CONTENTS

	Page
I. Introduction	299
II. Systematic descriptions	302
Phylum Archaeocyatha	302
Class Regularia Vologdin, 1937	302
Order Monocyathida Okulitch, 1935	302
Family Monocyathidae R. & W. R. Bedford, 1934 .	302
Genus *MONOCYATHUS* R. & W. R. Bedford, 1934	302
M. porosus R. & W. R. Bedford . . .	303
M. mellifer R. & W. R. Bedford . . .	303
Genus *TUMULIOLYNTHUS* Zhuravleva, 1963 .	304
T. irregularis (R. & W. R. Bedford) . .	304
Order AJACICYATHIDA R. & J. Bedford, 1939 . . .	305
Family DOKIDOCYATHIDAE R. & W. R. Bedford, 1936 .	305
Genus *ALPHACYATHUS* R. & J. Bedford, 1939 .	305
A. cf. annularis (R. & W. R. Bedford) . .	305
Family ACANTHINOCYATHIDAE R. & W. R. Bedford, 1936	306
Genus ACANTHINOCYATHUS R. & W. R. Bedford, 1936	306
A. apertus R. & J. Bedford	307
Family AJACICYATHIDAE R. & J. Bedford, 1939 . .	308
Genus *ARCHAEOCYATHELLUS* Ford, 1873 .	308
Subgenus *STAPICYATHUS* Debrenne, 1964 .	309
A. (S.) stapipora (Taylor) . . .	309
Genus *LOCULICYATHUS* Vologdin, 1931 . .	310
Subgenus *LOCULICYATHELLUS* nov. . .	310
L. (L.) floreus (R. & W. R. Bedford) .	310
Family ROBUSTOCYATHIDAE Debrenne, 1964 . . .	311
Genus *ROBUSTOCYATHUS* Zhuravleva, 1960 .	311
R. magnipora (R. & W. R. Bedford) . .	311
R. subacutus (R. & W. R. Bedford) . .	312
Genus *ZONACYATHUS* R. & J. Bedford, 1937 .	314
Z. retevallum (R. & W. R. Bedford) . .	315
Z. retezona (Taylor)	316
Family BRONCHOCYATHIDAE R. & J. Bedford, 1936 .	317
Genus *CYATHOCRICUS* nov.	318
C. tracheodentatus (R. & W. R. Bedford) .	319
C. dentatus (Taylor)	321
Family ETHMOCYATHIDAE nov.	322
Genus *ETHMOCYATHUS* R. & W. R. Bedford, 1934	323
E. lineatus R. & W. R. Bedford . . .	323

Family ERISMACOSCINIDAE Debrenne, 1964 . . . 325
  Genus *ERISMACOSCINUS* Debrenne, 1958 . . 325
    E. rugosus (R. & W. R. Bedford) . . . 325
    E. equivallum (Taylor) 326
    E. quadratus (R. & W. R. Bedford) . . 328
    E. textilis (R. & W. R. Bedford) . . . 329
    E. cellularis (R. & W. R. Bedford) . . 330
    E. petersi (R. & W. R. Bedford) . . . 331
    E. retifer (R. & W. R. Bedford) . . . 332
Family POLYCOSCINIDAE Debrenne, 1964 . . . 334
  Genus *TOMOCYATHUS* Rozanov, 1960 . . 334
    Subgenus *ERUGATOCYATHUS* nov. . . 334
      T. (E.) papillatus (R. & W. R. Bedford) 334
Family SALAIROCYATHIDAE Zhuravleva, 1955 . . 336
  Genus *SALAIROCYATHUS* Vologdin, 1940 . . 336
    Subgenus *S. (SALAIROCYATHUS)* Vologdin, 1940 336
      ? *S. (S.) annulatus* (R. & W. R. Bedford) 337
Family ALATAUCYATHIDAE Zhuravleva, 1955 . . 338
  Subfamily TUMULOCOSCININAE Zhuravleva, 1960 . 338
  Genus *ETHMOCOSCINUS* Simon, 1939 . . 338
    E. papillipora (R. & W. R. Bedford) . . 339
  Subfamily ALATAUCYATHINAE Zhuravleva, 1960 . . 340
  Genus *ALATAUCYATHUS* Zhuravleva, 1955 . 340
    Subgenus *ANAPTYCTOCYATHUS* nov. . . 340
      A. (A.) cribripora R. & W. R. Bedford . 340
      A. (A.) flabellus sp. nov. . . . 341
Class IRREGULARIA Vologdin, 1937 342
Order ARCHAEOCYATHIDA Okulitch, 1935 342
Family DICTYOCYATHIDAE Taylor, 1910 . . . 342
  Genus *PINACOCYATHUS* R. & W. R. Bedford, 1934 342
    P. spicularis R. & W. R. Bedford. . . 343
Family FLINDERSICYATHIDAE R. & J. Bedford, 1939 . 344
  Genus *FLINDERSICYATHUS* R. & J. Bedford, 1937 344
    Subgenus *FLINDERSICYATHUS* R. & J. Bedford, 1937 346
      F. (F.) graphicus (R. & W. R. Bedford). 346
      F. (F.) irregularis (Taylor) . . . 348
      F. (F.) major (R. & W. R. Bedford) . 349
      F. (F.) speciosus (R. & W. R. Bedford) . 350
    Subgenus *PYCNOIDOCYATHUS* Taylor, 1910 . 350
      F. (P.) synapticulosus (Taylor) . . 351
      F. (P.) simplex (Taylor) . . . 352
      F. (P.) maximipora (R. & W. R. Bedford) 352
      F. (P.) vicinisepta (R. & W. R. Bedford) . 353
Family METACYATHIDAE R. & W. R. Bedford, 1934 . 354
  Genus *METALDETES* Taylor, 1910 . . . 355
    M. dissepimentalis (Taylor) 358
    M. irregularis (R. & W. R. Bedford) . . 359
    M. taylori (R. & W. R. Bedford) . . . 360
  Genus *METAFUNGIA* R. & W. R. Bedford, 1934 . 361
    M. reticulata R. & W. R. Bedford . . 362
Family METACOSCINIDAE R. & W. R. Bedford, 1936 . 363
  Genus *METACOSCINUS* R. & W. R. Bedford, 1934 363
    M. reteseptatus R. & W. R. Bedford . . 364

? Family METACOSCINIDAE 367
Genus *PYCNOIDOCOSCINUS* R. & W. R. Bedford, 1936 367
P. pycnoideum R. & W. R. Bedford . . 367
III. STRATIGRAPHICAL CONCLUSIONS 368
IV. SUMMARY 371
V. ACKNOWLEDGMENTS 372
VI. REFERENCES 373
APPENDIX GLOSSARY 376

SYNOPSIS

Specimens from the Ajax Mine, first described by R. & W. R. Bedford (1934, 1936) and now in the British Museum (Natural History), have been re-examined and are revised. Fifteen families, 21 genera, 4 subgenera and 41 species are discussed and arranged according to current classification. One family (Ethmocyathidae), one genus (*Cyathocricus*), three subgenera (*Loculicyathellus*, *Erugatocyathus*, *Anaptyctocyathus*) and one species (*Anaptyctocyathus flabellus*) are considered new. The two genera *Metacyathus* and *Bedfordcyathus* are shown to be synonyms of *Metaldetes*. The excellent preservation of this silicified material has enabled the internal structures of some species to be determined accurately and resulted in the discovery of new wall and intervallum types.

Stratigraphical correlation shows that there are clear affinities between the Ajax, Kameshki and Sanashtygkol faunas. The presence of both advanced and simple forms in the Ajax fauna indicates that it is probably of Upper Kameshki–Lower Sanashtygkol age, i.e. the middle of the lower division of the Lower Cambrian.

Ce travail a pour but de reviser les Archéocyathes qui firent l'objet du premier mémoire de R. et W. R. Bedford (1934) et qui sont actuellement conservés dans les collections du B.M.(N.H.). 15 familles, 21 genres, 4 sous-genres et 41 espèces sont décrits et classés selon les critères actuels de classification. Une nouvelle famille (Ethmocyathidae), un nouveau genre (*Cyathocricus*), trois sous-genres (*Loculicyathellus*, *Erugatocyathus*, *Anaptyctocyathus*) et une nouvelle espèce ont été établies. *Bedfordcyathus* et *Metacyathus* tombent en synomymie avec *Metaldetes*. La fossilisation exceptionnelle du matériel silicifié a permis la définition de nouvelles structures murales et intervallaires.

Les faunes d'Ajax ont des affinités avec les faunes des horizons de Kameshki et Sanashtygkol, c'est à dire qu'elles datent du milieu de la partie inférieure du Cambrien inférieur.

I. INTRODUCTION

THE present work is a revision of material in the British Museum (Natural History) collection, collected and originally described by R. & W. R. Bedford in 1934. The specimens come from a Lower Cambrian exposure in a limestone hill behind the Ajax copper mine, ten miles north-east of Beltana, in the Flinders Range, South Australia. T. G. Taylor was the first to visit this locality in February, 1906 and his subsequent monograph on Australian Archaeocyatha (1910) was the first work to give detailed descriptions of such fossils.

In a series of papers from 1934–1939, the Bedfords, R., W.R. & J., described material collected in South Australia. The specimens mentioned in their papers now belong to the following museums, according to correspondence in the British Museum (Natural History) from Dr. Dorothy Hill: Memoir 1—B.M. (N.H.); Memoir 2—South Australian Museum; Memoirs 3, 4 and 6—Princeton University, U.S.A. The remain-

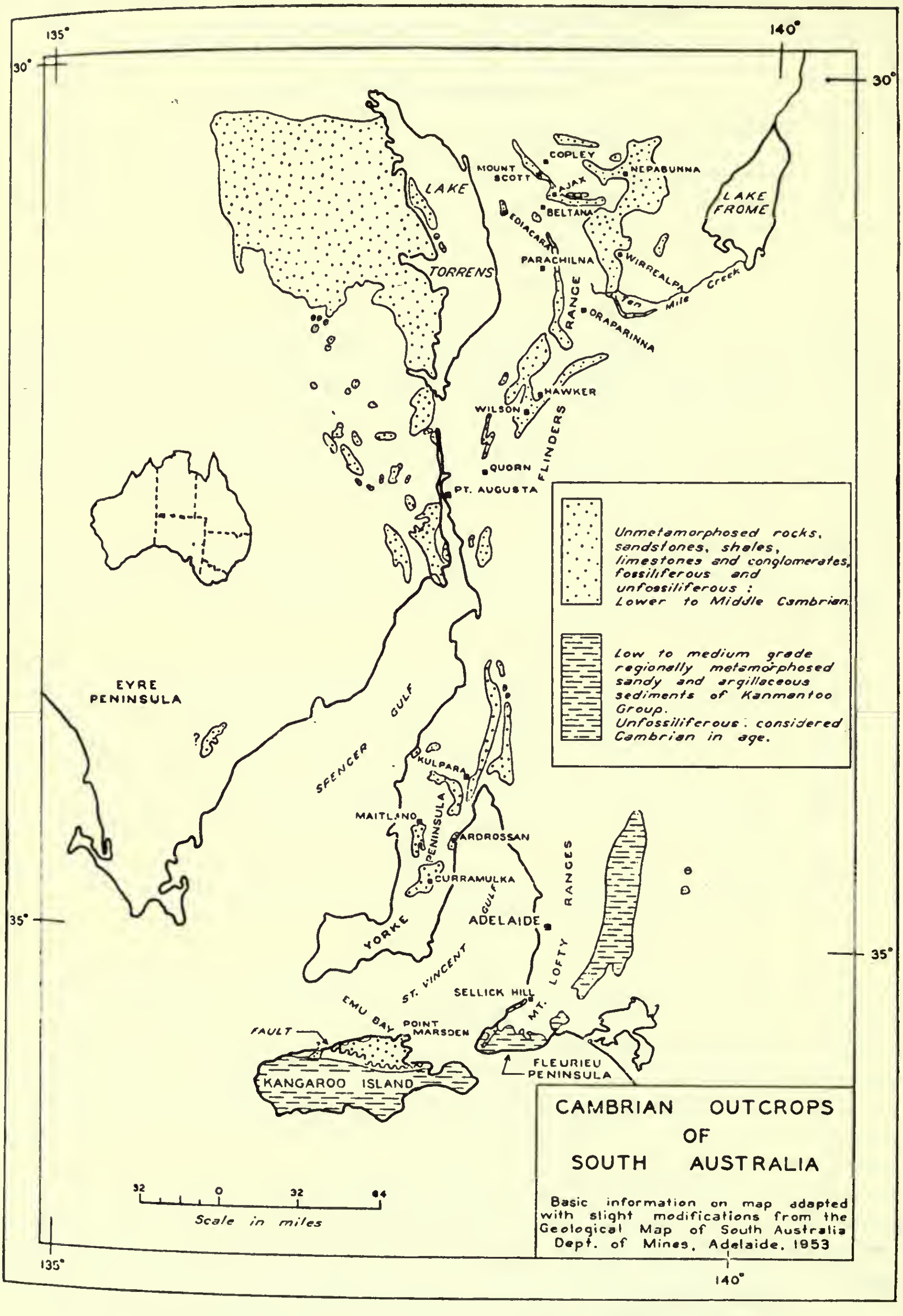
135°
140°
30°
30°
LAKE TORRENS
MOUNT SCOTT
COPLEY
NEPABUNNA
AJAX
BELTANA
EDIACARA
PARACHILNA
WIRREALPA
Ten Mile Creek
LAKE FROME
FLINDERS RANGE
ORAPARINNA
HAWKER
WILSON
QUORN
PT. AUGUSTA
Unmetamorphosed rocks, sandstones, shales, limestones and conglomerates, fossiliferous and unfossiliferous : Lower to Middle Cambrian
Low to medium grade regionally metamorphosed sandy and argillaceous sediments of Kanmantoo Group. Unfossiliferous : considered Cambrian in age.
EYRE PENINSULA
SPENCER GULF
KULPARA
MAITLAND
YORKE PENINSULA
ARDROSSAN
CURRAMULKA
MT. LOFTY RANGES
ADELAIDE
GULF ST. VINCENT
35°
35°
SELLICK HILL
EMU BAY
POINT MARSDEN
FAULT
KANGAROO ISLAND
FLEURIEU PENINSULA
CAMBRIAN OUTCROPS OF SOUTH AUSTRALIA
Basic information on map adapted with slight modifications from the Geological Map of South Australia Dept. of Mines, Adelaide, 1953
32 0 32 64
Scale in miles
135°
140°

FIG. 1. The Cambrian outcrops of South Australia. After B. Daily, 1956.

der of the Bedford collection was acquired by Prof. D. A. Brown of the Geology Dept, Australian National Museum, Canberra.

The silicified Australian material enabled both Taylor and the Bedfords to discover details of the finer internal structure by etching their specimens. Some credit is due to the Bedfords for the classification of the Archaeocyatha and their recognition of the systematic importance of ontogeny in such a classification.

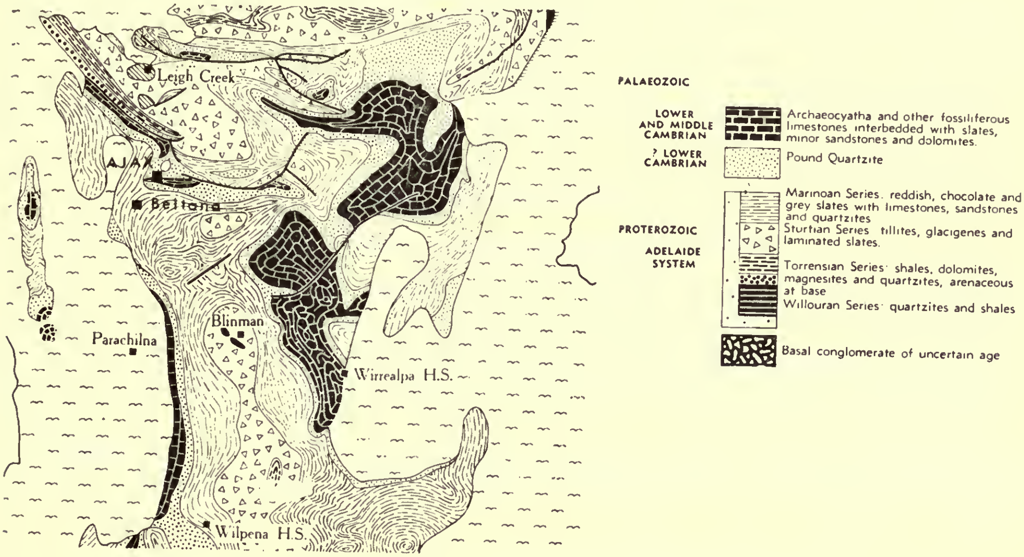
Leigh Creek
AJAX
Beltana
Blinman
Parachilna
Wirrealpa H.S.
Wilpena H.S.
PALAEOZOIC
LOWER AND MIDDLE CAMBRIAN
Archaeocyatha and other fossiliferous limestones interbedded with slates, minor sandstones and dolomites.
? LOWER CAMBRIAN
Pound Quartzite
PROTEROZOIC
ADELAIDE SYSTEM
Marinoan Series. reddish, chocolate and grey slates with limestones, sandstones and quartzites
Sturtian Series tillites, glacigenes and laminated slates.
Torrensian Series· shales, dolomites, magnesites and quartzites, arenaceous at base
Willouran Series· quartzites and shales
Basal conglomerate of uncertain age

FIG. 2. Section from a generalized geological map of the Flinders Ranges, produced by the Geol. Survey of South Australia and published in Glaessner, M. F. & Parkin, L. W. 1958.

The study of Archaeocyatha has figured prominently in assigning a Cambrian age to these rocks. Daily (1956) recognized 5 faunal assemblages in the Ajax limestones, but considered that the material collected by both Taylor and the Bedfords could only come from his faunal assemblage No. 1, which is given a Lower Cambrian age. Yet Walter (1967) states that the Ajax fauna cannot be placed in Daily's scheme of faunal units.

Recently Dorothy Hill (1965), in her work on Antarctic Archaeocyatha, revised the phylum and provided good illustrations of type material in Adelaide University, the South Australian Museum, Princeton University and the British Museum (Nat. Hist.). At her suggestion, I undertook the study of the Bedford material in the latter collection, with the intention of providing further description, re-classification and, above all, better figures of the specimens. It has often been difficult in the past to assess the characters of genera and species mentioned by the Bedfords, as their figures are either composite, or cannot be located on the actual specimen. The genus *Syringocnema* is not dealt with in this paper, although well represented in that part of the Bedford collection in the B.M. (N.H.), because of its thorough description by both Taylor (1910 : 153) and Gordon (1920 : 699).

" Archaeocyatha are known from all the continents except South America and are characteristic of the calcareous facies of the Lower Cambrian " (Hill 1965 : 30). This widespread distribution makes them particularly useful for stratigraphical correlation; yet, as Walter (1967) points out, their use is limited for, being benthonic, dispersal is restricted. " Recognition of the extinct Archaeocyatha as a separate phylum near the Porifera and Coelenterata, is now general " (Hill 1965 : 45). In the past, their systematic position has been the subject of considerable debate, with opinion ranging from calcareous algae to sponges. However, they are regarded by Hill (1964 : 253) " as single multicellular organisms, with organization higher than that of the Protozoa, but with less differentiation than the Porifera ".

A short glossary of the more important descriptive, morphological terms is included as an Appendix.

II. SYSTEMATIC DESCRIPTIONS

Phylum ARCHAEOCYATHA Vologdin, 1937

Class *REGULARIA* Vologdin, 1937

Order MONOCYATHIDA Okulitch, 1935

Family ***MONOCYATHIDAE*** R. & W. R. Bedford, 1934

DIAGNOSIS. Single-walled cup. Pore system simple to slightly complex.

COMPOSITION OF THE FAMILY. *Monocyathus* Bedford, R. & W.R. 1934, *Rhabdolynthus* Zhuravleva 1960, *Tumuliolynthus* Zhuravleva 1963, ? *Tunkia* Bedford, R. & J. 1936.

Genus ***MONOCYATHUS*** R. & W. R. Bedford, 1934

1899 *Rhabdocyathus* von Toll (*non* Brooks 1893): 45, pl. 8, figs. 2c, 6 and 7, t.-figs. 4–7.
1910 *Archaeolynthus* Taylor : 157, pl. 5.
1934 *Monocyathus* R. & W. R. Bedford : 2, pl. 1, fig. 1.
1936 *Monocyathus* R. & W. R. Bedford : 12, pl. 10, fig. 46.
1937 *Rhabdocnema* Okulitch : 251
1939 *Monocyathus* R. & W. R. Bedford; R. & J Bedford : 69, pl. 42, fig. 161.
1939 *Archaeolynthus* Taylor; Simon : 21.
1949 *Archaeolynthus* Taylor; Zhuravleva : 549.

TYPE SPECIES. *Monocyathus porosus* R. & W. R. Bedford, 1934, selected by R. & W. R. Bedford, 1936.

DISCUSSION. Okulitch (1950), Debrenne (1964) and Hill (1965) consider *Archaeolynthus* Taylor 1910 an invalid name, as the type specimen was not designated by the author and the reference material was destroyed by serial sectioning.

DIAGNOSIS. Small conical cups with a simple porous single wall and the vertical rows of pores in a quincunx pattern.

COMPOSITION OF THE GENUS. *Monocyathus absolutus* (Vologdin 1940), *M. bilateralis* (Vologdin 1962), *M. contractus* Hill 1965, *M. copulatus* (Vologdin 1940), *M. kuzneskii* (Vologdin 1931), *M. lebedevae* (Vologdin 1937), *M. macrospinosus* (Zhuravleva 1963), *M. mellifer* R. & W. R. Bedford, 1936, *M. nalivkini* (Vologdin 1939), *M. operculatus*

Maslov 1960, *M. partibus* (Vologdin 1963), *M. polaris* (Vologdin 1937), *M. porosus* R. & W. R. Bedford, 1934, *M. robustus* R. & W. R. Bedford, 1936, *M. sibiricus* (von Toll 1899), *M. simplex* (Vologdin 1940), *M. sparsipora* R. & W. R. Bedford, 1936, *M. spinosus* R. & W. R. Bedford, 1936, *M. tenuimurus* (Vologdin 1940), *M. tolli* (Krasnopeeva 1937), *M. unimurus* (Vologdin 1940).

Monocyathus porosus R. & W. R. Bedford

(Pl. 1, fig. 3)

1934 *Monocyathus porosus* R. & W. R. Bedford : 2, pl. 1, fig. 1.
1939 *Monocyathus porosus* R. & J. Bedford : 69, fig. 161.
1963 *Archaeolynthus porosus* (Bedford & Bedford); Zhuravleva : 88–89, fig. 39.
1965 *Monocyathus porosus* R. & W. R. Bedford; Hill : 52, pl. 2, fig. 1.

LECTOTYPE. B.M. (N.H.) S 4140 selected by Hill (1965).

OTHER MATERIAL. Syntypes B.M. (N.H.) S 7630–31, S 4783–8.

DESCRIPTION. Conical cup, slightly waved, with a single wall of constant thickness and pores in quincunx. The upper edge, in the material studied, is not turned back into the central cavity as an incipient pelta. The pores are proportionately smaller and more numerous towards the upper part of the cup. The bigger specimens have smaller and more regular pores.

DIMENSIONS

	Lectotype (mm.)	S 7630–7631 (mm.)
Height (*pars*)	15	31
Diameter	6	9·5
Wall:		
Diameter of the pores	0·27–0·20	0·10
Distance between the vertical rows	0·33–0·27	0·33
Distance between the horizontal rows	0·54–0·67	0·35

DISCUSSION. This species is very similar to the Siberian species *M. nalivkini* (Vologdin). Zhuravleva (1963 : 80) distinguishes the two, mainly on the supposed presence of a pelta and inner rugosity in *porosus*, which was described and figured by R & W. R. Bedford (1936). However, these peculiar structures are neither seen in the lectotype, nor on the other specimens in the British Museum collection. It is therefore possible that the two species are synonymous.

Monocyathus mellifer R. & W. R. Bedford

(Pl. 1, fig. 4)

1936 *Monocyathus mellifer* R. & W. R. Bedford : 12, pl. 10, fig. 49.

MATERIAL. B.M. (N.H.) S 4821. The whereabouts of the holotype is not known.

REMARKS. The specimen is a cylindrical fragment of a single-walled cup. The wall is like a honeycomb, formed by short hexagonal pipes with a hexagonal section on the outer side and a circular section on the inside.

DIMENSIONS

	(mm.)
Height (pars)	16
Diameter	3·72
Wall:	
Inner diameter of pores	0·40
Pipe wall thickness	0·27
Wall thickness	0·67

DISCUSSION. This fragmentary piece is similar to the type-species briefly described by R. & W. R. Bedford 1936.

Genus ***TUMULIOLYNTHUS*** Zhuravleva, 1963

1932 *Rhabdocyathus* von Toll : Vologdin (pars) : 65.
1963 *Tumuliolynthus* Zhuravleva : 101.

TYPE SPECIES. *Rhabdocyathus tubexternus* Vologdin 1932, by original designation Zhuravleva (1963 : 101).

DIAGNOSIS. One-walled Archaeocyatha, with the pores protected externally by simple tumuli.

COMPOSITION OF THE GENUS. (After Zhuravleva 1963): *T. irregularis* (R. & W. R. Bedford, 1934), *T. karakolensis* Zhuravleva 1963, *T. musatovi* (Zhuravleva 1961), *T. tubexternus* (Vologdin 1932), *T. vologdini* (Yakovlev 1956).

Tumuliolynthus irregularis (R. & W. R. Bedford)

(Pl. 1, fig. 1)

1934 *Monocyathus irregularis* R. & W. R. Bedford : 2, pl. 1, fig. 2.
1939 *Monocyathus irregularis* R. & W. R. Bedford; R. & J. Bedford : 68, fig. 160.
1963 *Tumuliolynthus irregularis* (R. & W. R. Bedford) Zhuravleva : 110, fig. 58.

HOLOTYPE. B.M. (N.H.) S 4141.

OTHER MATERIAL. B.M. (N.H.) S 7643–6, S 4771, S 4774–7, S 4764–5.

REMARKS. The holotype is a small cylindrical fragment with several large apertures, each of which is probably the basal trace of a pore. The scattered tumuli occur on the lower parts and have a large opening at the top. The poor preservation and small size of this specimen prevent a more detailed description. The other specimens are more complete, generally larger, and have a thicker wall with irregular apertures, each with a tumulus perforated at the top.

DIMENSIONS

	S 4141 (mm.)	S 4774–4777 (mm.)	S 4817–4820 (mm.)
Cup:			
Height	6·1	..	18
Diameter	1·69	0·33	0·27
Wall:			
Diameter of pores	0·60–0·23	0·20	0·27
Average distance between pores	..	0·67	..
Thickness	0·10	0·33	0·27

Discussion. R. & W. R. Bedford, (1934) and R. & J. Bedford, (1939) noted the presence of " papillae " and only placed this species in the genus *Monocyathus* provisionally. Zhuravleva (1963) uses the term " tumulus " when referring to the papillae and after examining the material, I consider her change of terminology justified.

Tumuliolynthus irregularis differs from other species of the genus by the irregular size and pattern of its pores.

Order AJACICYATHIDA R. & J. Bedford, 1939

Family ***DOKIDOCYATHIDAE*** R. & W. R. Bedford, 1936

Diagnosis. Two-walled cup, walls simply porous, connected by radial horizontal rods.

Composition of the Family, *Dokidocyathus* Taylor 1910, *Alphacyathus* R. & J. Bedford, 1939.

Genus ***ALPHACYATHUS*** R. & J. Bedford

1939 *Alphacyathus* R. & J. Bedford : 72.

Type Species. *Dictyocyathus annularis* R. & W. R. Bedford, 1936, by original designation R. & J. Bedford, (1939 : 72, fig. 55).

Diagnosis. Cup with two simply porous walls. In the intervallum, radial cylindrical bars are arranged in regularly spaced horizontal planes and are connected by synapticulae that are opposite from loculus to loculus, forming a continuous ring in the centre of the intervallum.

Composition of the Genus. A single species *Alphacyathus annularis* (R. & W. R. Bedford, 1936).

Alphacyathus cf. ***annularis*** (R. & W. R. Bedford)

(Pl. 1, fig. 2)

cf. 1936 *Dictyocyathus annularis* R. & W. R. Bedford : 13, pl. 11, fig. 55.
1939 *Alphacyathus annularis* R. & W. R. Bedford) R. & J. Bedford : 72.

Holotype. P 942 in the South Australian Museum, Adelaide according to Hill (1965 : 55).

Other Material. B.M. (N.H.) S 4822, S 4766.

Description. Small cylindrical cups. Outer wall is pierced by circular pores in quincunx, the skeletal tissue between the pores (" linteaux ") is of constant thickness and equal in width to the pore diameter. Inner wall is built on the same pattern with regular pores and considerable skeletal tissue. One inner wall pore at each interradial space and at each horizontal level.

DIMENSIONS

	S 4822 (mm.)	S 4766 (mm.)
Cup:		
Height	5	unknown
Diameter	2	2·45
Intervallum	0·70	0·50
Central cavity	0·56	0·90
Outer wall:		
No. of pores between 2 bars	2–3	2–3
Diameter	0·07	0·07
Vertical partitions	0·07	0·07
Horizontal partitions	0·07	0·07
Thickness	0·07	0·07
Inner wall:		
No. of pores between 2 bars	1	1
Diameter	0·15	0·13
Vertical partitions	0·07	0·15
Horizontal partitions	0·07	0·15
Thickness	0·07	0·15
Rods:		
Interradial space	..	0·2
Vertical space	0·2	..
Diameter	0·15	0·15

DISCUSSION. Neither specimen provides a sufficiently complete transverse section for showing the synapticulae and they cannot be assigned with certainty to *annularis*.

Family ***ACANTHINOCYATHIDAE*** R. & W. R. Bedford, 1936

DIAGNOSIS. Two-walled cups with intervallar horizontal rods. Inner wall simple, but outer wall has protected pores, the lower skeletal part of each pore bearing a long spinous process, projecting upwards and outwards from the wall.

COMPOSITION OF THE FAMILY. *Acanthinocyathus* R. & W. R. Bedford, 1934.

Genus ***ACANTHINOCYATHUS*** R. & W. R. Bedford, 1936

1934 *Acanthocyathus* R. & W. R. Bedford (non Edwards & Haime 1848, which is a hexacoral) : 4.
1936 *Acanthinocyathus* R. & W. R. Bedford : 11.

TYPE SPECIES. *Acanthocyathus apertus* R. & W. R. Bedford (1934 : 4, fig. 20), by monotypy.

DIAGNOSIS. Two-walled cups with radial, horizontal, or upwardly oblique rods. The outer wall pores are partly obscured by scales. The inner wall consists of a net of polygonal to circular pores.

COMPOSITION OF THE GENUS. *A. apertus* (R. & W. R. Bedford), ? *A. transiens* R. & J. Bedford 1939.

Acanthinocyathus apertus R. & W. R. Bedford

(Pl. 2, Text-fig. 3)

1934 *Acanthocyathus apertus* R. & W. R. Bedford : 4, fig. 20.
1936 *Acanthinocyathus apertus* (R. & W. R. Bedford); R. & W. R. Bedford : 11, fig. 45.

LECTOTYPE. B.M. (N.H.) S 4166 chosen here.

OTHER MATERIAL. Para-lectotypes B.M. (N.H.) S 4167–8.

DESCRIPTION. Cylindrical rods cross the intervallum and are orientated horizontally, or sometimes obliquely upwards and outwards from the inner to the outer wall. The inner wall is well shown in S 4168; it consists of a large pored net, with a mesh of irregular size and shape formed by skeletal threads of constant thickness. The outer wall is the most characteristic feature of this species; the large pores are in quincunx and of various shapes; the skeletal tissue occupies a smaller area than the pores and carries long spines that are directed upwards and outwards. Unfortunately, these long protective spines are often broken, but when complete they may reach the centre of the overlying pore, that is to say, since the rows alternate, the centre of the pore two rows above. The base of the spine is level with the lower third of the pore.

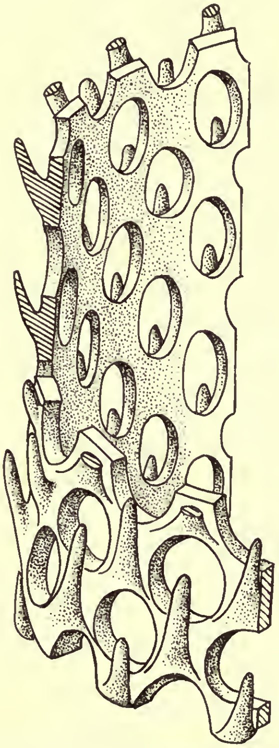

FIG. 3. *Acanthinocyathus apertus* R. & J. Bedford

Dimensions

	Holotype S 4166 (mm.)	S 4168 (mm.)	S 4167 (mm.)
Cup:			
Height (pars)	34	32	25
Upper diameter	17·5	13	11
Lower diameter	15	12·5	8·5
Upper intervallum	3·5	3·4	3
Lower intervallum	3·4	3·4	2·37
Outer wall:			
Diameter of pores	1·7–2	..	1·01–1·35
scales	4·75–6	..	3–4
Vertical partitions	1·35	..	0·67
Horizontal partitions	1·35	..	1·35
Thickness	0·67	..	0·6
Inner wall:			
Diameter of pores	0·75	0·27–2·03	0·6–1·15
Partitions	+	0·61	0·4
Thickness	0·40	0·47	0·4
Rods	0·4	..	..

Discussion. R. & W. R. Bedford, thought the inner wall was a scaffolding of triradiate spicules, the side rays surrounding the pores and the median ray being prolonged into a spinous process directed upwards and outwards. They considered that the spicular elements of *Acanthinocyathus* could indicate a phylogenetic link between Sponges and Archaeocyatha. This suggestion is not borne out by observation. The wall of *Acanthinocyathus* is a porous sheet with the elongation of its horizontal skeletal parts into scales of an unusual size.

Family ***AJACICYATHIDAE*** R. & J. Bedford, 1939

Genus ***ARCHAEOYCATHELLUS*** Ford, 1873

Subgenus ***STAPICYATHUS*** Debrenne, 1964

1873 *Archaeocyathellus* Ford (Pars).
1964 *Archaeocyathellus* (*Stapicyathus*) Debrenne : 127.

Type Species. *Archaeocyathus stapipora* Taylor (1910 : 118), by original designation of Debrenne (1964 : 127).

Diagnosis. Conical cups; outer and inner walls with simple pores as in true Ajacicyathidae. Intervallum crossed by imperforate radial septa. The neighbouring loculi only open into one another and into the central cavity, by the stirrup-pores of the inner wall.

Remarks. Debrenne (1964 : 127) considered this form a non-corrugated subgenus of *Archaeocyathellus* Ford.

Composition of the Subgenus. *A.* (*S.*) *stapipora* (Taylor 1910) and ? *A.* (*S.*) *yukonensis* (Okulitch 1957).

Archaeocyathellus* (*Stapicyathus*) *stapipora (Taylor)

(Pl. 1, fig. 5)

1910	*Archaeocyathus stapipora* Taylor : 118, pl. 7, figs. 37 and 38, pl. 3, fig. 10, t-fig. 14.
1939	*Archaeocyathus stapipora* Taylor; R. & J. Bedford : 75.
1939	*Archaeocyathus* (*Protocyathus*) *stapipora* (Taylor) Simon : 54.
1964	*Archaeocyathellus* (*Stapicyathus*) *stapipora* (Taylor) Debrenne : 127.
1965	*Robustocyathus stapipora* (Taylor) Hill : 61 and 68.

LECTOTYPE. Taylor 1910, Pl. 7, fig. 38 G, chosen here. The specimen should be in the University of Adelaide.

OTHER MATERIAL. B.M. (N.H.) S 4733, S 4351–2, S 4138, S 4528, S 4817–20, S 7621.

DESCRIPTION. Narrow intervallum of constant width from the basal conical apex to the upper bowl-shaped cup. Some specimens are more cylindrical. Outer wall thin, pierced by round pores that are arranged quincunxially. Inner wall thicker, with one vertical row of pores in front of each septa; each pore is excavated into its septum so that stirrup-pores are formed. These inner wall pores are also arranged into horizontal lines.

DIMENSIONS

	S 4733 (mm.)	S 4351 (mm.)	S 4352 (mm.)	S 4817–4820 (mm.)	S 7621 (mm.)
Cup:					
Height (pars)	30	40	22	15	20
Diameter	about 40	about 20	about 12	about 35	about 10
Intervallum coeff.	0·02	0·45–0·66	0·1	0·042	0·1
Interseptum	0·339	0·61	0·61	0·74	0·37
Loculi	1/3·4	from 1/1·8 to 1/2	1/2	1/2	1/3·3
Outer wall:					
No of pore rows per interseptum	3	3	3	3 to 4	3
Diameter of pores	0·07	0·07	0·06	0·075	0·07
Vert. partitions	0·068	0·068	0·07	0·068	0·1
Thickness	0·150	0·23	0·15	0·1	0·1
Inner wall:					
No. of pore rows per interseptum	two 1/2	two 1/2	two 1/2	two 1/2	two 1/2
Diameter of pores	0·27	0·27	0·20	0·27	0·27
Vertical part.	0·27	0·33	0·33	0·40	0·27
Horizontal part	0·16	0·27	0·20	0·27	0·20
Thickness	0·1	0·1	0·1	0·1	0·1
Septa	non porous	non porous	non porous	non porous	non porous
Thickness	0·06	0·06	0·07	0·07	0·07

DISCUSSION. Only one species known. The different shapes i.e. cylindrical, or bowl-shaped could conceivably represent different species, but their coefficients are not sufficiently different.

Genus *LOCULICYATHUS* Vologdin, 1931

Subgenus *LOCULICYATHELLUS* nov.

TYPE SPECIES. *Archaeocyathus floreus* R. & W. R. Bedford 1934.

DIAGNOSIS. Cup has the generic characters of *Loculicyathus*: thin porous walls and septa, vesicular tissue crossing intervallum and central cavity. The external longitudinal corrugations on the outer wall, like those of *Ajacicyathellus*, subgenus of *Ajacicyathus* (see Debrenne 1964 : 127), or *Archaeocyathellus* Ford 1873, distinguish it as a subgenus.

DISCUSSION. R. & W. R. Bedford (1937) compared *A. floreus* with *Archaeocyathellus*. They singled out forms with radial imperforate septa and stirrup-pores at the inner wall, from others with regularly porous septa. The holotype of *floreus* (S 4144), the paratype and other material in the B.M. (N.H.) collection, show sparse pores but no stirrup-pores.

The only species recognized at present is *Loculicyathus* (*Loculicyathellus*) *floreus* (R. & W. R. Bedford 1934).

Loculicyathus* (*Loculicyathellus*) *floreus (R. & W. R. Bedford)

(Pl. 3, figs. 1, 2, 4)

1934 *Archaeocyathus floreus* R. & W. R. Bedford : 2, fig. 4.
1937 *Archaeocyathus floreus* R. & W. R. Bedford; R. & J. Bedford : 35, figs. 144A & B.

HOLOTYPE. B.M. (N.H.) S 4144.

OTHER MATERIAL. Paratype B.M. (N.H.) S 4145. Also B.M. (N.H.) S 4730, S 4739 and S 7635.

DIAGNOSIS. Small cylindrical cup with vertical corrugation between two neighbouring septa, so that transverse sections recall scleractinian corolla. Outer wall with horizontal and vertical rows of non-alternating pores. The pores of the inner wall and septa are in quincunx. A few dissepiments occur across the intervallum and central cavity.

DIMENSIONS

	S 4144 (mm.)	S 4145 (mm.)	S 4739 (mm.)
Cup:			
Height (pars)	9·5	10	..
Diameter	low 5·0 upp. 6·0	low 5·0 upp. 6·5	6·77
Interseptum	0·75–2·0	0·75–2·0	0·95
Interv. coeff.	0·4	..	1·6
Parietal coeff.	1·0	..	1·6
Outer Wall:			
No. of pore rows per intersept	6	..	..
Diameter of pores	0·13	..	..
Vertical skel. part.	0·13	..	..
Horizontal skel. part.	0·33	..	..

DIMENSIONS—*continued*

	S 4144 (mm.)	S 4145 (mm.)	S 4739 (mm.)
Inner Wall:			
No. of pore rows per intersept	2	..	..
Diameter of pores	0·23	0·26–0·37	..
Vertical skel. part.	0·33	0·35	..
Horizontal skel. part.	0·23	0·22	..
Septa:			
Diameter of pores	0·23	0·30	..
Vertical skel. part.	0·33	..	..
Horizontal skel. part.	0·23	0·26	..

DISCUSSION. The specimens from Ardrossan figured by R. & J. Bedford, (1939, figs. 144 A & B) only have one pore per intersept at the inner wall and a non-corrugated outer wall. They would therefore, seem to be a quite different form.

Family *ROBUSTOCYATHIDAE* Debrenne, 1964

Genus *ROBUSTOCYATHUS* Zhuravleva, 1960

TYPE SPECIES. *Archaeocyathus robustus* Vologdin 1937, by original designation of Zhuravleva (1960 : 133).

DIAGNOSIS. Solitary cups with simply porous outer wall and single vertical row of apertures per intersept at the inner wall, so that each loculus opens into the central cavity.

COMPOSITION OF THE GENUS. *R. argentus* (Okulitch 1935), *R. annulatus* Zhuravleva 1960, *R. artecaveatus* (Vologdin 1940*a*), *R. biohermicus* Zhuravleva 1960, *R. densus* Debrenne 1964, *R. hupei* Debrenne 1964, *R. levigatus* (Vologdin 1940*a*), *R. magnipora* (R. & W. R. Bedford 1934), *R. moori* (Vologdin 1937), *R. novus* Zhuravleva 1960, *R. polyseptatus* (Vologdin 1940*a*), *R. proskurjakowi* (von Toll 1889), *R. pseudotichus* (Vologdin 1940*a*), *R. salebrosus* (Vologdin 1931), *R. spinosus* Zhuravleva 1960, *R. subacutus* (R. & W. R. Bedford, 1934), *R. sucharichensis* Zhuravleva 1960, *R. ? tenuis* (Vologdin 1940).

Robustocyathus magnipora (R. & W. R. Bedford)

(Pl. 3, fig. 5)

1934 *Archaeocyathus magnipora* R. & W. R. Bedford : 2, pl. 1, fig. 7.
1937 *Paranacyathus magnipora* (R. & W. R. Bedford) R. & J. Bedford : 34.

HOLOTYPE. B.M. (N.H.) S 4146.

DESCRIPTION. The holotype, a partially destroyed cup, was the only specimen examined. The radial septa are few, straight and pierced by three alternate vertical rows of circular pores, which are not connected to the wall pores. The outer wall is a thin plate with circular pores in quincunx. The inner wall has a single vertical row of large pores per intersept and pores of neighbouring rows alternate. The septa, which spring out of the inner wall, form boundaries to new pores by splitting the previous one.

DIMENSIONS

Cup:	(mm.)
Height (pars)	24
Diameter	8·8
Intervallum	1·83
Interseptum	0·74
Loculus (trapezoid)	0·47 and 0·6 for Height = 0·9
Parietal coefficient	+ unknown
Outer wall:	
Vertical rows of pores per intersept	4
Diameter of pores	0·20
Skeletal partitions	0·13
Thickness	0·13
Inner wall:	1
Vertical diameter	0·40
Horizontal diameter	0·60
Skeletal partitions	0·33
Thickness	0·33
Septa:	
Alternating vertical rows of pores per septum	3
Diameter	0·61
Skeletal partitions	0·61

DISCUSSION. The specimens figured by R. & J. Bedford (1937, figs 142A–E) and described as *magnipora* are unlike the holotype mentioned above. They differ by having various forms and patterns of outer wall and septal pores. These characters, together with the presence of an *Archaeopharetra*-type apex, caused R. & J. Bedford to place *magnipora* in the genus *Paranacyathus*. Unfortunately, it was not possible to compare the holotype with these specimens. The holotype (S 4146) shows the true characters of *Robustocyathus*: regular walls and septal pores, which are sufficient to place it in the Class Regularia, although the initial stages are not present in the specimen. At the moment, it is not possible to decide the true systematic position of the specimens figured by the Bedfords in 1937.

Robustocyathus subacutus (R. & W. R. Bedford)

(Pl. 3, figs. 6, 7, Text-fig. 4)

1934 *Archaeocyathus subacutus* R. & W. R. Bedford : 2, pl. 1, figs. 3a–c.
1937 *Archaeocyathus acutus* Bornemann; Ting : 358, pl. 9, figs. 1–2.
1961 *Ajacicyathus walliseri* F. & M. Debrenne : 696, pl. 19, fig. 3.

HOLOTYPE. B.M. (N.H.) S 4142.

OTHER MATERIAL. B.M. (N.H.) S 4143, S 4747, S 4792, S 7620.

DESCRIPTION. Small cylindrico-conical cup with thin skeletal plates and few pores. The outer wall only has one pore in the middle of each intersept; these pores are arranged in widely separated vertical rows and more closely set horizontal ones. The inner wall is thin and perforated by a single row of pores per intersept. The aperture of each pore is larger than the width of the interseptum. The inner edges of the septa, which laterally delineate the pore, have vertical undulations (see Text-fig. 4). Numerous radial septa, having a few small isolated pores, are found near the outer wall, but they have only been seen in specimen S 4747.

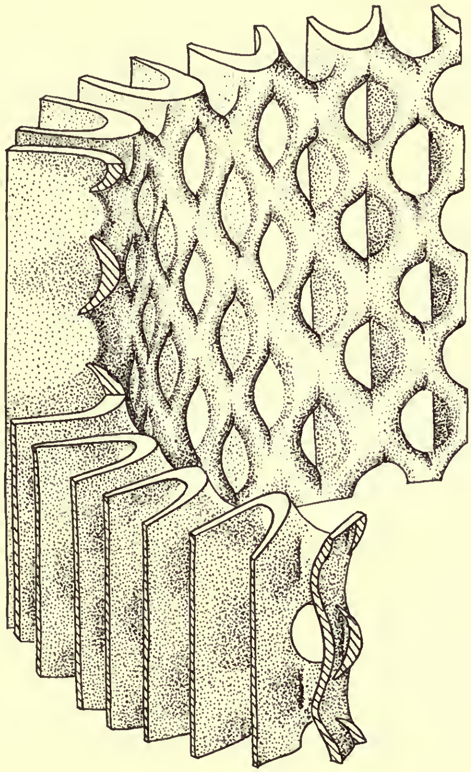

FIG. 4. *Robustocyathus subacutus* (R. & W. R. Bedford)

The undulations on the inner edges of the septa, close to the inner wall, are different from those seen in *Ethmophyllum* Meek. The amplitude of the waves is smaller, while the sinuous edges do not join together to close up the interseptum and form another wall that connects the septa, but simply limit the inner wall pores. The inner wall, itself, remains as a completely separate sheet.

DIMENSIONS

	S 4142 (mm.)	S 4143 (mm.)	S 4747 (mm.)	S 7620 (mm.)	*walliseri* (mm.)
Cup:					
Height (pars)	30	20	25	+	+
Diameter	10–12	+	8–10	7	13
Intervallum coeff.	0·3	0·39	0·5	..	0·23
Parietal coeff.	5·4	+	5·5	5·5	5·2
Interseptum	0·30	0·33	0·20	0·25	..
Loculus	1/6	1/8	1/7	..	1/4
Outer wall:					
No. of pore rows per intersept	1	+	+	1	1
Diameter	0·13	..	..	0·7	0·13
Skeletal vert. part.	0·40	..	..	0·40	+
Skeletal horiz. part.	0·13	..	..	0·13	0·11
Thickness	0·06	..	0·06	0·07	0·07
Inner wall:					
No. of pore rows per intersept	1	1	1	1	1
Diameter	0·33	0·40	0·27	0·27	0·26
Skeletal vert. part.	0·13	0·13	+	0·13	0·13
Skeletal horiz. part.	0·13	0·13	+	0·13	+
Thickness	0·33	0·40	0·33	0·27	0·26
Septa					
Thickness	0·10	0·10	+	0·10	0·06

DISCUSSION. *R. walliseri* Debrenne, in spite of its very large size, seems to fall between the limits of specimens of *subacutus*. Another species, *R. pseudotichus* (Vologdin) has similar undulations on the inner parts of the septa that border the large inner wall pores, but in addition, has long spines on the vertical edges of the pores.

Genus *ZONACYATHUS* R. & J. Bedford, 1937

1937 *Zonacyathus* R. & J. Bedford : 36.
1940a *Ethmophyllum* Meek; Vologdin (*pars*) : 66–68.

TYPE SPECIES. *Archaeocyathus retevallum* R. & W. R. Bedford (1934 : 2, fig. 6), by monotypy.

DIAGNOSIS. Porous two-walled cups with no, or few, porous radial septa. The outer wall has regular pores. The inner wall has branching pore-tubes; the initial tube is located in the middle of each interseptum and then branches so that the secondary tubes open in front of the septa. The tubes may lengthen and curve into the central cavity. The pore-tubes are never formed by septal fluting.

DISCUSSION. The type species *retevallum* is known from only the three specimens in the B.M. (N.H.) collection. The skeletal tissue is extremely thin and breakable, with the result that structures are either crushed or destroyed, making it difficult to distinguish the pore systems. The validity of a genus based on such fragments may be questionable. Nevertheless, from studying a very close but simpler species, *Z. retezona* Taylor, which has an inner wall built of shorter pore-tubes that branch in the same way, it is possible to understand the more complex pattern present in *retevallum*.

COMPOSITION OF THE GENUS. *Zonacyathus retevallum* (R. & W. R. Bedford 1934), *Z. retezona* (Taylor 1910). The species *Ethmophyllum poletevae* Vologdin 1940*a*, *E. vermiculatum* Vologdin 1938 and *E. flexum* Vologdin 1940*a*, are placed in *Zonacyathus* with reservation.

Zonacyathus retevallum (R. & W. R. Bedford)

(Pl. 4, figs. 4, 5)

1934 *Archaeocyathus retevallum* R. & W. R. Bedford : 2, fig. 6.
1937 *Zonacyathus retevallum* (R. & W. R. Bedford,) R. & J. Bedford : 36, figs. 153A–E.
1965 *Zonacyathus retevallum* (R. & W. R. Bedford): Hill : 76, pl. 4, figs. 3a–b.

HOLOTYPE. B.M. (N.H.) S 4147.

OTHER MATERIAL. B.M. (N.H.) S 4726–4727.

DESCRIPTION. Bowl-shaped cup with narrow waved intervallum, easily distorted but without giving any obvious folds. Owing to the bad preservation of the material, all measurements are approximate and observations incomplete.

Outer wall simple with two alternating rows of oval pores, arranged in quincunx, to each interseptum. The septa are difficult to see in longitudinal section in the Bedford specimens. The septa appear to be imperforate, but may have small scattered pores. The inner wall has branching pore-tubes of Y-form, which lengthen and curve into the central cavity. It is suspected that some lateral communication occurs between the pore-tubes that penetrate into the central cavity.

DIMENSIONS

	S 4147 : 1 (mm.)	S 4147 : 2 (mm.)	S 4726–4727 (mm.)
Cup:			
Height	25	40	..
Diameter	20	12–30	10
Intervallum coefficient	0·11	0·12	0·2
Parietal coefficient	..	6·6	..
Interseptum	0·27	0·27	0·27
Loculus	1/7·2	1/4·8	1/5·5
Outer wall:			
No. of rows of pores per intersept	2	2	..
Diameter of pores	..	0·13×0·06	..
Vertical partitions	..	0·10	..
Horizontal partitions	..	0·10	..
Thickness	0·10	0·13	0·10
Inner wall:			
No. of rows of pores per intersept	1	1	1
Diameter of pores	0·20	0·27	0·20
Vertical partitions	0·10	0·13	0·13
Horizontal partitions	0·10	0·13	0·13
Thickness	at least 0·6	0·8	0·6
Septa:			
Thickness	..	0·10	0·10

Discussion. *Ethmophyllum flexum* Vologdin (1940*a* : 66, pl. 15, fig. 4) is very similar to *Z. retevallum* R. & W. R., Bedford, having the same irregular shape and size.

Zonacyathus retezona (Taylor)

(Pl. 4, figs. 1, 2, 3, Text-fig. 5)

1910 *Archaeocyathus retezona* (Taylor) : 121, pl. 7, fig. 38A, pl. 6, fig. 31E.

Material. B.M. (N.H.) S 4353, S 4764, S 4774, S 4778, S 4803–4808, S 4811–4816, S 7623, S 7634, S 4731.

Description. Conical, externally smooth cups. The outer wall is a porous sheet, with vertical alternating rows of slightly elliptical pores surrounded by skeletal tissue of constant width. Radial septa are, probably, imperforate. Inner wall independent from septa and has two vertical rows of pores, one row opposite each septa and the other in the middle of each interseptum. Each pore opposite a septum, is the opening for two oblique pore-tubes, one coming from each loculus. On the inner face of the intervallum, a central, radial pore-tube is joined by a branch from each of its neighbours to form one elliptical pore. All of these pore-tubes are horizontal. *Z. retezona*

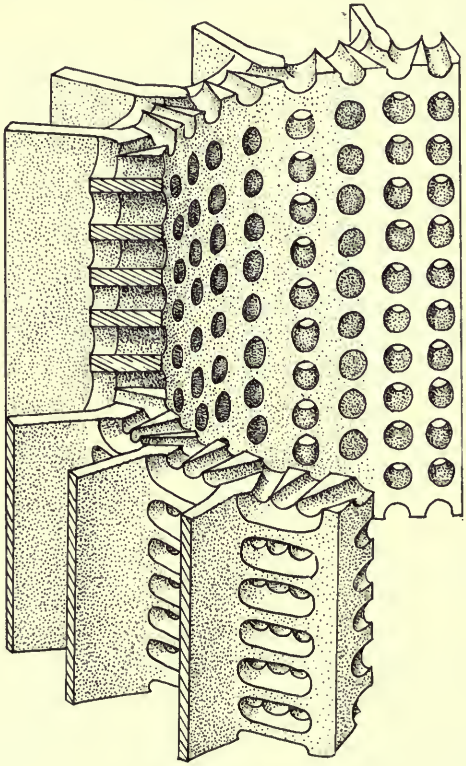

Fig. 5. *Zonacyathus retezona* (Taylor)

differs from *Z. retevallum* because its tubes are short and do not lengthen, or curve into the central cavity.

DIMENSIONS

	S 4353 (mm.)	S 7623 (mm.)	S 4811–4816 (mm.)	S 4730–4732 (mm.)	S 4764 (mm.)	S 4774–4777 (mm.)	S 7634 (mm.)	S 4778 (mm.)
Cup:								
Height	20	..	45	42	20	pars 15	..	13
Diameter	10	8	15	27	5–8	9	10	10
Intervallum coeff.	0·21	0·22	0·12	0·9	0·3	0·25	0·21	0·21
Loculus	1/3	1/3	1/3	1/3	1/2	1/3	1/3	1/3
Parietal coeff.	3·9	4·2	..	..	4·8 to 3·9	..	3·4	..
Outer wall:								
No. or rows of pores per intersept	4	4	3	4	4–6	4–6	4–6	4
Diameter of pores	0·06	..	0·10	0·06	0·07	..	..	0·07
Vertical partitions	0·07	..	0·07	0·06	0·06	..	..	0·05
Horizontal partitions	0·06	..	0·06	0·07	0·06	..	..	..
Thickness	0·13	0·13	0·13	0·13	0·10	..	0·13	..
Inner wall:								
No. of rows of pores per intersept	1	1	1	1	1	1	1	1
Diameter of pores	0·20–0·27	0·27	0·13–0·2	0·27	0·27	..	0·27	0·20
Vertical partitions	0·16	0·13	0·10	0·13	0·13	..	0·16	..
Horizontal partitions	0·13	..	0·13	0·20	0·20	..	..	0·13
Thickness	0·40	0·40	0·35	0·40	0·40	..	0·54	0·40
Septa:								
No. of pore rows	0	..	2	?	1	..	..	..
Diameter of pores	..	..	0·13	0·13	..	..	..	..
Partitions	..	..	0·13	0·33	..	..	..	..
Thickness	0·07	0·10	0·10	0·10	..	..	0·06	0·07

DISCUSSION. Taylor (1910 : 122) gave the following interpretation of the inner wall of *Z. retezona*: " a simply porous inner wall, with one or two pores between each pair of adjacent septa ". In fact, if one refers to his fig. 27, it is seen that one pore occurs in each septum and the other in the middle of the interseptum. I consider that the regular inner wall is composed of pore tubes, that join together and open into the central cavity. Taylor thought the inner parts of the septa were modified into curved rods which supported the simple inner wall. However, the excellent silicified material in the Bedford collection enables the path of the canals to be followed throughout their length.

Family **BRONCHOCYATHIDAE** R. & J. Bedford, 1936

1936 Bronchocyathidae R. & J. Bedford : 25
1937 Stillicidocyathidae Ting : 367.
1951 Thalamocyathidae Zhuravleva : 98.
1955 Ethmophyllidae Okulitch : E 12.
1959 Cyclocyathellidae Zhuravleva : 426.
1965 Bronchocyathidae R. & J. Bedford; Hill : 93.

TYPE GENUS. *Thalamocyathus* Gordon 1920 (=*Bronchocyathus* R. & J. Bedford, 1936).

COMPOSITION of GENUS. *Thalamocyathus* Gordon 1920, *Stillicidocyathus* Ting 1937. *Polystillicidocyathus* Debrenne 1959, *Cyathocricus* gen. nov.

REMARKS. Thalamocyathidae Zhuravleva 1951 has not won general acceptance under Article 40*a* of the International Code of Zoological Nomenclature, 1961 and while this rule stands in its present form, this family name must be rejected.

Genus ***CYATHOCRICUS*** nov.

TYPE SPECIES. *Archaeocyathus tracheodentatus* R. & W. R. Bedford, 1934.

DERIVATION. From *κρικος*, *cricos* = a ring.

DIAGNOSIS. Cup with a simply porous outer wall; straight, sparsely perforated radial septa and an annulate inner wall. Annuli consist of undulating, horizontal, or slightly inclined plates that are neither S-, nor V-shaped; their axial rim is cogged.

COMPOSITION OF THE GENUS. *C. tracheodentatus* (R. & W. R. Bedford 1934), *C. dentatus* (Taylor 1910) and *C. annulispinosus* (Vologdin 1931).

DISCUSSION. *Cyathocricus* differs from other annulate genera in that the rings appear to be straight in vertical section. The β component, closest to the septa, is generally horizontal and the α component, projecting into the central cavity, is complicated by cogs that are more or less fused together.

This new genus is established for those species incorrectly referred to the genus *Bronchocyathus* R. & J. Bedford 1936. Hill (1965 : 94) gives an account of this situation, involving *Thalamocyathus* and *Bronchocyathus*.

Gordon (1920 : 687) created the genus *Thalamocyathus* and included the species *Archaeocyathus tubavallum* Taylor, *A. trachealis* Taylor, *A. infundibulum* Bornemann, *A. ichnusae* Meneghini and *T. flexuosus* Gordon, but did not designate a type species.

R. & J. Bedford (1936 : 25) erected *Bronchocyathus*, designating *B. trachealis* (Taylor) as the type species and including *Ethmophyllum dentatum* Taylor and *Archaeocyathus tracheodentatus* R. & W. R. Bedford.

The type species of *Thalamocyathus* Gordon was subsequently designated by Ting (1937 : 368) as *T. trachealis* (Taylor), after elimination of the other syntype species because they possessed cribrose inner walls. Hill (1965 : 94) states that she considers this to be a valid designation. Simon (30th Dec. 1939 : 40) later named *A. trachealis* as the type species of the genus, in case of any doubts that Ting had done so.

Thus *Bronchocyathus* R. & J. Bedford, is a junior objective synonym of *Thalamocyathus* Gordon since both have the same type species (Int. Code Nomen., Article 61b).

R. & J. Bedford (1939 : 75) pointed out that *A. trachealis* Taylor belonged to *Cyclocyathus* Vologdin 1931, a genus of which they were unaware in 1936. As Vologdin had not designated a type species, they cited *trachealis*, but this is not acceptable since the species was not listed in the original description of *Cyclocyathus*, although the Bedfords considered that Vologdin's use of *tubavallum* Taylor was a *lapsus calami* for *trachealis* Taylor. In referring to *tubavallum*, the Bedfords mentioned that it was the first species listed by Gordon in his description of *Thalamocyathus* and was founded on a single fragment of which conflicting figures were provided, and that the whereabouts of the specimen is uncertain. Finally, R. & J.

Bedford (1939 : 75) decided to apply the name *Bronchocyathus* to those forms having a more complex inner wall than *Cyclocyathus* and gave *Ethmophyllum dentatum* Taylor as the type species. This does not conform to the rules of zoological nomenclature, for Article 61 states "the type of any taxon, once fixed in conformity with the provisions of the Code, is not subject to any change except by exercise of the plenary powers of the Commission ". It is, therefore, necessary to provide another name for the genus containing *dentatum* Taylor. *Archaeocyathus tracheodentatus* R. & J. Bedford, is selected as the type species of the new genus *Cyathocricus*, as it is more thoroughly known than *dentatum*.

Hill (1965 : 94) mentions other nomenclatural problems of *Thalamocyathus* and the species *trachealis* Taylor. Zhuravleva (1960 : 220) cites *Bronchocyathus* as the genus of the family Bronchocyathidae, distinguishing this group from the Stillicidocyathidae by the presence of inter-communicating pore-tubes. However, this was based on the use of *E. dentatum* Taylor as type-species of *Bronchocyathus*.

Cyathocricus tracheodentatus (R. & W. R. Bedford)

(Pl. 5, figs. 4, 5, Pl. 6, fig. 4, Text-fig. 6)

1934 *Archaeocyathus tracheodentatus* R. & W. R. Bedford : 2, fig. 5.
1936 *Bronchocyathus tracheodentatus* (R. & W. R. Bedford) R. & J. Bedford : 25, fig. 104.

HOLOTYPE. B.M. (N.H.) S 4148.

OTHER MATERIAL. B.M. (N.H.) S 4754.

DESCRIPTION. The type specimen is a conical cup with a broken apex. Corrugations on the upper part provide good tangential and longitudinal sections of the inner wall (see Text-fig. 6). The numerous radial septa are straight and are perforated by a few vertical rows of fine pores. Part of the outer wall is preserved, showing the somewhat irregularly placed polygonal pores. The inner wall consists of a vertical series of thick, horizontal, ring-shaped plates, which are triangular in cross-section and are joined to the inner edges of the septa by the β component. The annuli thin toward the central cavity, are slightly wavy on their upper face and their free rim (α component) is regularly cogged.

DIMENSIONS

	S 4148 (Upper) (mm.)	S 4148 (Lower) (mm.)	S 4754–4755 (mm.)
Cup:			
Height (pars).	31	31	5
Upper Diameter	11	6·5	7
Lower Diameter	0·2	0·3	0·3
Parietal coefficient	..	8·3	..
Interseptum	0·27	0·13	0·13
Loculus	0·27/1·6	0·13/1·29	..
Outer wall:			
No. of pore rows per intersept	3–4	..	2
Diameter	0·06	0·06	0·05
Vertical partitions	0·05	0·05	0·05
Horizontal partitions	0·05	0·05	0·05
Thickness	0·10	0·10	0·13

DIMENSIONS—*continued*

	S 4148 (Upper) (mm.)	S 4148 (Lower) (mm.)	S 4754–4755 (mm.)
Inner wall:			
Space between rings	0·27	..	0·20
Thickness of ring	0·13–0·20	..	0·10
Length of cog	0·67	..	0·67
Width of ring	0·33	..	0·27
Space between cogs	0·5	..	..
Septa:			
No. of pores	Imperforate	..	Imperforate
Thickness	..	0·06	0·05

DISCUSSION. *C. annulispinosus* (Vologdin 1931) is similar morphologically, but its specific coefficients are not well known. According to Vologdin (1931 : fig. 42) the diameter is approximately 5·6 mm, the intervallum coefficient would be 0·4 and the parietal coefficient 12—figures that are quite close to those of specimen S 4148. The essential difference is in the downward orientation of the annuli into the central cavity present in *annulispinosus*.

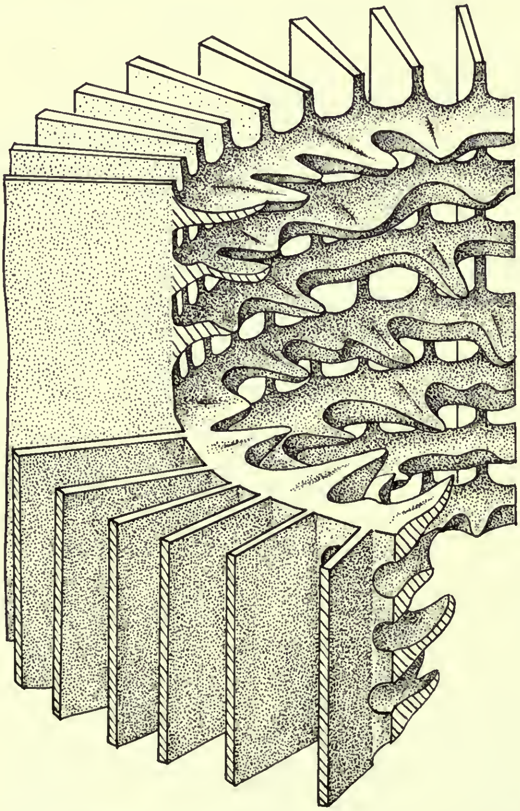

FIG. 6. *Cyathocricus tracheodentatus* (R. & W. R. Bedford)

Cyathocricus dentatus (Taylor)

(Pl. 6, figs. 1–3, Text-fig. 7)

1910 *Ethmophyllum dentatum* Taylor : 129, pl. 10, fig. 59; pl. 13, fig. 76; pl. 16, fig. 89; t.-figs. 23 and 31.
1936 *Bronchocyathus dentatus* (Taylor) R. & J. Bedford : 25, fig. 103.
1960 *Bronchocyathus dentatus* (Taylor); F. & M. Debrenne : 703, pl. 20, fig. 8.

HOLOTYPE. Not designated.

OTHER MATERIAL. B.M. (N.H.) S 4752–4753, S 4756, S 4355.

DESCRIPTION. Cylindrical-conical cup that may have a large diameter and a wide central cavity. The intervallum is full of straight radial septa, that have about 2–3 vertical rows of small pores near the outer wall. The outer wall is perforated by pores of the same size as those of the septa, with 2–3 alternate vertical rows per interseptum. There are no stirrup-pores connecting the two systems. The inner wall is formed by a series of vertical annular plates, which are as thick as the septa. These plates extend into the inner part of the intervallum, as well as into the central cavity.

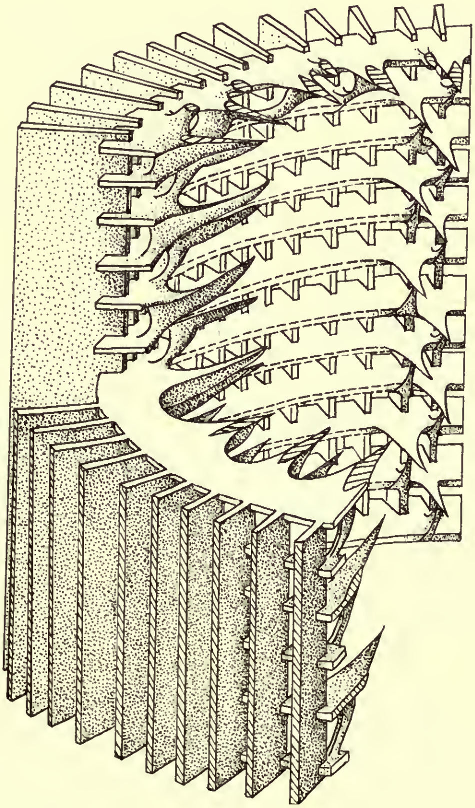

FIG. 7. *Cyathocricus dentatus* (Taylor)

Their free edge is serrated into toothlike projections, that are 2–3 loculi wide at the base, and which are situated either in front of a septum, or in the centre of an interseptum (Pl. 6, fig. 2). The tips of these projections are flat on top and bend slightly upwards. When examining the material, layers of the teeth were prised apart without discovering any order of appearance. On the lower part of each tooth there is a curved support which joins it to the underlying ring plate.

Dimensions

	S 4355 (mm.)	S 4753 (mm.)	S 4756 (mm.)	S 4752 (mm.)
Cup:				
Height	17	30	53	..
Diameter	12	18	15–16	9
Intervallum coefficient	0·3	0·15	0·5	..
Interseptum	0·13	0·20	..	0·13
Outer wall:				
No. of pore rows per intersept	2	2–3	not seen	..
Diameter	0·06	0·06	..	..
Vertical partitions	0·05	0·05	..	..
Horizontal partitions	0·05	0·05	..	..
Thickness	0·06	0·06	0·06	0·13
Inner wall:				
Distance between annuli	0·20	0·27	0·20	0·20
Thickness of annuli	0·06	0·06	0·06	0·10
Width of annuli	0·40	0·33	0·27	0·33
Projections	0·40	0·67	0·27	0·67
Septa:	Imperforate	Perforate on outer side	Imperforate	
Thickness	0·06	0·06	..	0·05
Diameter	..	0·06	..	..
Vertical partitions	..	0·06	..	..
Horizontal partitions	..	0·27	..	..

Discussion. The interpretation of the inner wall structure of *dentatus* is difficult owing to the limited number of known specimens. In common with other forms, the term " vesicular " has been used in the past to describe the various poor oblique sections of specimens, which have a complex inner wall structure. It was not possible to examine the holotype, but there are specimens of *dentatus* in the Bedford collection, wrongly called *tracheodentatus*, which provided various views of this structure. From these specimens (S 4355, S 4753 and S 4752) it was possible for me to reconstruct the inner wall of *dentatus* with some certainty. This species differs from *tracheodentatus* and *annulispinosus* by having thinner annuli, vertical supports between the annuli, and the triangular shape and different distribution of the teeth.

Family **ETHMOCYATHIDAE** nov.

Diagnosis. Simple outer wall; uniserially pored inner wall covered over on the innermost (central cavity) side with a secondary wall of annular plates. This feature is characteristic of the new family. *Ethmocyathus* R. & W. R. Bedford is the type genus.

DISCUSSION. It is necessary to create a separate family within the Ajacicyathacea to place the genus *Ethmocyathus*. There is no justification for placing *Ethmocyathus* in the family Ethmophyllidae (Hill 1965 : 76; Zhuravleva 1960 : 162), for its inner wall is not formed by horizontal fluting of the inner edges of the septa, as they suggested. Neither is the genus a doubtful member of the Tumulocyathidae (Debrenne 1964 : 113), since the outer wall has simple pores and its annuli have a peculiar form.

Genus ***ETHMOCYATHUS*** R. & W. R. Bedford, 1934

1934 *Ethmocyathus* R. & W. R. Bedford : 2, fig. 8.

TYPE SPECIES. *Ethmocyathus lineatus* R. & W. R. Bedford, by monotypy.

DESCRIPTION. Cup with straight radial, sparsely porous septa. The outer wall has close, simple pores. The inner wall is composed of a thin sheet of hexagonal pores screened from the central cavity by thin, narrow horizontal annuli.

DISCUSSION. Sometimes, both of the horizontal sides of the inner wall hexagonal pores are reduced so that the openings become rhombic. The inner edges of the septa are sinuous, following the outlines of the inner wall pores, but do not contribute to their formation by horizontal fluting.

COMPOSITION OF THE GENUS. *Ethmocyathus lineatus* R. & W. R. Bedford.

Ethmocyathus lineatus R. & W. R. Bedford

(Pl. 5, figs., 1–3, Text-fig. 8)

1934 *Ethmocyathus lineatus* R. & W .R. Bedford : 2, fig. 8.
1965 *Ethmocyathus lineatus* R. & W. R. Bedford; Hill : 76, pl. 4, figs. 2a–b, t.-fig. 16. 2.

HOLOTYPE. B.M. (N.H.) S 4149.

DESCRIPTION. This is based on a single specimen consisting of a fragment from a, probably, cylindrical cup. Radial septa with sparse pores on the outer two-thirds of each septum. The annular plates join the inner wall net of hexagonal pores, without any visible thickening. The outer wall is simple with regular oval pores.

DIMENSIONS

Cup:	(mm.)
Height (pars).	15
Diameter (approx.)	13
Interseptum	0·18
Intervallum coefficient	0·13
Outer wall: (only seen between 2 neighbouring septa)	
3 pores lengthened horizontally and arranged in quincunx	
Diameter	0·05–0·03
Skeletal partitions	0·03
Thickness	0·07

DIMENSIONS—*continued*

	(mm.)
Inner wall:	
Vertical diameter	0·27
Horizontal diameter	0·2
Skeletal partitions	0·075
Thickness	0·37
Thickness of annuli	0·03
Distance between annuli	0·03
5 annular plates cover one pore (vertically)	
Septa:	
Imperforate for 0·37 mm. from the inner wall	
Diameter of pores	0·03
Vertical partitions	0·15
Horizontal partitions	0·18

DISCUSSION. Only this one species known.

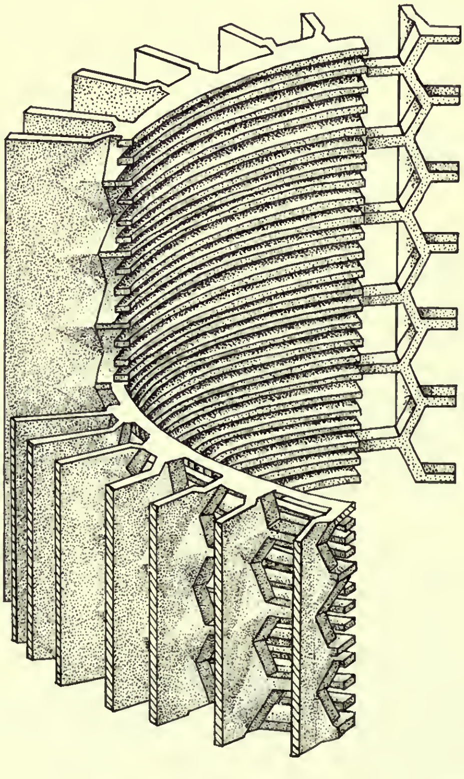

FIG. 8. *Ethmocyathus lineatus* R. & W. R. Bedford

Family **ERISMACOSCINIDAE** Debrenne, 1964

Diagnosis. Cup with radial septa and porous tabulae. Thin, simply porous outer wall. Inner wall with several vertical series of pores to each interseptum, sometimes with thickening of the pore framework (" linteaux ") and ornamental spines.

Composition of the Family. *Erismacoscinus* (*Pluralicoscinus*) Debrenne 1963, *Erismacoscinus* Debrenne 1958, *Asterocyathus* Vologdin 1940, *Retecoscinus* Zhuravleva 1960, *Tuvacyathus* Vologdin 1940, *Geniculicyathus* Debrenne 1960, *Coscinoteichus* Debrenne 1964, *Coscinoptycta* Broili 1915.

Genus ***ERISMACOSCINUS*** Debrenne, 1958

Type Species. *Erismacoscinus marocanus* Debrenne 1958 : 65, pl. 3, figs. 11–16, by monotypy.

Diagnosis. Intervallum with regularly porous septa and tabulae. Simple outer wall, generally perforated by numerous openings in quincunx. Thick inner wall, always has several vertical series of pores to each interseptum. The inner wall pores frequently carry spines, that vary in shape and distribution.

Composition of the Genus. *Erismacoscinus* contains all those species, having several vertical series of pores to each interseptum, that were previously included in the genus *Coscinocyathus* Bornemann (see list of Debrenne 1964 : 166–167).

Discussion. Hill (1965 : 108–109) suggests this genus might be synonymous with *Tannuolacyathus* Vologdin 1957, but the vesicular tissue and double porous wall of the latter, have led me to consider that genus as belonging to a distinct family, the *Tannuolacyathidae* (Debrenne 1964 : 188).

Erismacoscinus rugosus (R. & W. R. Bedford)

(Pl. 8, figs. 2, 3)

1934 *Coscinocyathus rugosus* R. & W. R. Bedford : 3, fig. 11.
1964 *Erismacoscinus rugosus* (R. & W. R. Bedford) Debrenne : 167.

Holotype. B.M. (N.H.) S 4152.

Description. A single specimen of a funnel-shaped cup with a wide intervallum and rather narrow central cavity. Septa simply porous and not always reaching the inner wall. Tabulae form a regular network of pores. The inner wall is simple with some spines. The pores of the outer wall are in vertical rows, between which the " linteaux " project. These keels continue towards the exterior, giving the fossil a rough appearance from which its specific name is derived. The pores of neighbouring rows alternate slightly.

DIMENSIONS

	(mm.)
Cup:	
Height (pars).	6
Diameter	from 4·75–5·5
Interseptum (outer)	1·01
(inner)	0·33
Intertabulum	1·35
Loculi	1/2, 8/2, 8
Intervallum coefficient	0·8
Parietal coefficient	3·6
Outer wall:	
2–3 rows of pores per interseptum	
Vertical diameter of pores	0·20
Horizontal diameter of pores	0·30
Vertical thickness	0·13
Horizontal thickness	0·05
Inner wall:	
2 rows of alternating pores per interseptum	
Diameter of pores	0·10
Linteaux	0·16
Thickness of wall	0·10
Septa:	
10 rows of pores per septum	
Diameter of pores	0·05
Partitions	0·15
Tabulae:	
7 pores per interseptum	
Diameter of pores	0·05
Skeletal partitions	0·06

DISCUSSION. The presence of outer keels is a rare modification. It seems that *E. equivallum* (Taylor) has outer keels in front of each septum (see below).

Erismacoscinus equivallum (Taylor)

(Pl. 7, figs. 1–3 and 5)

1908 "turbinate Archaeocyathinoid" Taylor : 426, pl. 1, fig. 1.
1910 *Coscinocyathus equivallum* Taylor : 138–139, pl. 15, fig. 85, t.-fig. 12.
1964 *Erismacoscinus equivallum* (Taylor) Debrenne : 167

HOLOTYPE. In the University of Adelaide.

OTHER MATERIAL. B.M. (N.H.) S 200 is the counterpart (i.e. the other face of the section) of the holotype. S 198, naturally etched specimen figured by Taylor (1908, pl. 1, fig. 2 : 423).

DESCRIPTION. Outer wall has projections of skeletal tissue corresponding to the septa. As I did not see a specimen entirely free of matrix, it is only possible to assume that this feature is similar to the keels present in *E. rugosus*. These projections only occur at the junction of the septa and the outer wall, and not between the rows of pores in the interseptum. The pores are elliptical and in quincunx.

The inner wall has round, alternate pores. The linteaux are smooth on the intervallum side but small projections of spines and " bristles " occur on the central cavity face.

Thick, straight septa have round regularly scattered pores in elongated quincunx. The skeletal tissue occupies a greater surface area than the pores. Slightly convex tabulae have a fine network of small, more or less regular polygonal pores.

DIMENSIONS

	S 200 (mm.)	S 198 (mm.)
Cup:		
Height	22	..
Diameter	10	30–18
Intervallum coefficient	0·46	0·43
Parietal coefficient	Not measurable	66
Interseptum	0·37	0·41
Intertabulum	0·44	..
Outer wall:		
No. of pore rows per intersept	2	2
Diameter of pores	0·15	0·22–0·15
Vertical partitions	0·11	0·11–0·15
Horizontal partitions	0·15	0·11
Thickness	0·11	0·11
Inner wall:		
No. of pore rows per intersept	2	2
Diameter of pores	0·07	0·15
Vertical partitions	0·07	0·11
Horizontal partitions	0·07	0·11
Thickness	0·11	0·11
Septa:		
No. of pore rows per intersept	9–10	15
Diameter of pores	0·11	0·07
Vertical partitions	0·15	0·22
Horizontal partitions	0·15	0·22
Thickness	0·07	0·15
Tabulae:		
No. of pore rows per intersept	14	4–22
Diameter of pores	0·05	0·05–0·15
Vertical partitions	0·05	0·03–0·07
Horizontal partitions	0·05	..
Thickness	0·07	0·07

DISCUSSION. Specimen S 198 is somewhat corrugated. At the level of the folds the septa are not radial but parallel, as seen in *Polystillicidocyathus* Debrenne and other colonial forms.

The similarity in structure of the two walls is not quite so evident as Taylor stated (1910 : 138). The specimen S 200 shows that the inner wall is a little thinner and has ragged " linteaux " and spines.

Erismacoscinus quadratus (R. & W. R. Bedford)

(Pl. 7, fig. 4, Pl. 8, fig. 5)

1934 *Coscinocyathus quadratus* R. & W. R. Bedford : 3, pl. 2, fig. 10.
1964 *Erismacoscinus quadratus* (R. & W. R. Bedford) Debrenne : 167.

HOLOTYPE. B.M. (N.H.) S 4157.

DESCRIPTION. Only one incomplete specimen known; a little deformed and therefore, difficult to measure accurately or to calculate the specific coefficients.

The septa and tabulae form a sub-quadrate network of irregular shape, due to the slight waving of the intervallum plates. They both have isolated, simple, round pores arranged in quincunx. The outer wall also has simple pores in quincunx but with the majority often lengthened horizontally. The inner wall is smooth on the intervallum side, but irregular and with spines around the pores on the central cavity face. The pores are arranged in horizontal rows and alternate from one row to another.

DIMENSIONS

	Lower section (mm.)	Upper section (mm.)
Cup:		
Height	25	
Diameter	11	16
Intervallum	2·64	2·64
Interseptum	0·37–0·50	0·37
Intertabulum	0·30–0·60	..
Intervallum coefficient	0·38	0·2
Parietal coefficient	probably 3·1	..
Outer wall:		
3–4 rows of pores per intersept		
Diameter of pores	0·07–0·15	..
Partitions	0·11	..
Thickness	0·05	..
Inner wall:		
2–3 rows of pores per intersept		
Diameter of pores	0·11–0·13	..
Septa:		
20 pores per loculus		
Diameter of pores	0·03	..
Partitions	0·11	..
Thickness	0·05	..
Tabulae:		
3 rows of 20 pores per loculus		
Diameter of pores	0·03	..
Partitions	0·06	..
Thickness	0·15 (with the spines)	..

DISCUSSION. The peculiar features of the inner wall (smooth in the intervallum, spined in the central cavity) have previously been described for *E. rugosus* (R. & W. R. Bedford) and *E. equivallum* (Taylor)—two species that differ from *quadratus* in other characters.

Okulitch (1948 : 343) compared *rhyacoensis* and *quadratus*, as both have subquadrate loculi. However, the American species has pore-tubes in the outer wall; an inner wall which is typical of *Coscinocyathus*, with a single pore series to each interseptum; and an intervallum with vesicular tissue as well as tabulae.

Erismacoscinus textilis (R. & W. R. Bedford)

(Pl. 9, figs. 1–4)

1934 *Coscinocyathus textilis* R. & W. R. Bedford : 3, pl. 2, below fig. 11.
1964 *Erismacoscinus textilis* (R. & W. R. Bedford) Debrenne : 167.

HOLOTYPE. B.M. (N.H.) S 4155.

PARATYPE. B.M. (N.H.) S 4156.

DESCRIPTION. The holotype has a cylindro-conical cap that tapers gently in its lower parts. The intervallum consists of quadrate to rectangular loculi, limited by radial septa and flat, irregularly-spaced tabulae.

The outer wall has a single vertical series of pores per interseptum (in a large interseptum there are two rows, but these soon become separated by a new septum). The pores of the outer wall are much larger than those of the inner wall, they are also horizontally lengthened and the rows alternate. Pores of the inner wall are very small and arranged in quincunx. Septa and tabulae are regularly porous. Skeletal tissue is well-developed.

The paratype is a fragment of a large, bell-shaped cup, with a narrow intervallum in which the different pore characters of the two walls can easily be compared. The inner wall has a regular net of round pores in quincunx, whilst the outer wall has 1–2 rows of pores. Domes of vesicular tissue are present in several loculi.

DIMENSIONS

	S 4155 (Upper) (mm.)	S 4155 (Lower) (mm.)	S 4156 (mm.)
Cup:			
Height:	30		43
Diameter	10	6	36 (Chord)
Intervallum	1·32	1·32	2
Interseptum	0·40	0·35	0·62
Intertabulum	0·6–2·71	irregular	2·70–4·70
Parietal coefficient	4·2	3·3	..
Outer wall:			
No. of rows of pores per interseptum	1–2	1–2	1–2
Diameter	0·34–0·15	0·34–0·15	0·15
Skeletal partitions	0·11	0·11	0·15
Horizontal partitions	0·07	..	0·15
Thickness	0·95	..	0·15
Inner wall:			
No. of pore rows per interseptum	3–4	..	4
Diameter	0·07	..	0·10
Vertical partitions	0·07	..	0·10
Horizontal partitions	0·07	..	0·10
Thickness	0·11	.	0·07

DIMENSIONS—*continued*

	S 4155 (Upper) (mm.)	S 4155 (Lower) (mm.)	S 4156 (mm.)
Septa:			
No. of rows of pores	8	..	10
Diameter	0·11	..	0·10
Vertical partitions	0·15	..	0·10
Thickness	0·07	..	0·10
Tabulae:			
No. of pores per interseptum	4–5	4	5
Diameter	0·07	0·07	0·05
Vertical partitions	0·07	0·07	0·07
Horizontal partitions	..	..	0·07
Thickness	0·05	0·05	0·10
Vesicular tissue:	..	..	0·03

DISCUSSION. The two specimens, a cylindrical one and a bowl-shaped one, are placed in the same species. More material is needed in order to decide whether they belong to separate species, or not. Generally the outer wall of Archaeocyatha is thinner than the inner one. However, in this species the opposite is the case. It is impossible to recognize the correct position of a fragment, if one only has the pore characters of a wall to go by. Another example of this difficulty is the case of *Coscinocyathus unilinearis* R. & W. R. Bedford (see Pl. 13, fig. 4), and *Coscinoptycta convoluta* (Taylor). If the wall with a single pore, is the inner wall, then *Coscinoptycta* is a synonym of *Coscinocyathus* and *unilinearis* is a species of *Coscinocyathus*. On the other hand, if it is the outer wall that has one pore, then *Coscinoptycta* remains a separate genus and *unilinearis* is a species of *Erismacoscinus*.

Erismacoscinus cellularis (R. & W. R. Bedford)

(Pl. 8, figs. 1 and 4)

1934 *Coscinocyathus cellularis* R. & W. R. Bedford : 3, pl. 3, fig. 16.

HOLOTYPE. S 4162 B.M. (N.H.).

DESCRIPTION. The holotype is a longitudinally broken fragment of an almost cylindrical cup, showing the porosity of the different skeletal plates.

The outer wall is a thin, regular and finely porous plate with horizontally elongated pores. The inner wall is thicker, consisting of small, regular polygonal tubes that face upwards; its central cavity face has several spines, or other outgrowths, arising from the pore walls.

The septa have small evenly-spaced pores. The tabulae are close together with their convex side uppermost, they are also finely perforated but the pores are more numerous than those of the septa.

DIMENSIONS

	(mm.)
Cup:	
Height	55
Diameter	20
Intervallum	3
Intertabulum	1–1·32
Interseptum	0·30
Intervallum coefficient	0·75
Parietal coefficient	not measurable
Outer wall:	
No. of pore rows per interseptum	2
Diameter	0·15–0·07
Vertical partitions	0·07
Horizontal partitions	0·11
Thickness	0·07
Inner wall:	
No. of pore rows per interseptum	3
Diameter	0·15; 0·11; 0·11 (nr. central cavity)
Vertical partitions	0·11
Thickness	0·26
Septa:	
No. of pore rows per interseptum	30 approx.
Diameter	0·03
Vertical partitions	0·11
Horizontal partitions	0·08
Thickness	0·07
Tabulae:	
No. of pore rows per interseptum	3–4
Diameter	0·05
Vertical partitions	0·07
Horizontal partitions	0·07
Thickness	0·07

DISCUSSION. R. & W. R. Bedford (1934 : 3) suggested that the outer wall is covered by a thin membrane that has very minute pores, but I could not find any evidence of this structure. Their " irregular mosaic " of the inner wall is, in fact, the result of the modification of the skeletal tissue (" linteaux ") into barbs and spines. The regular polygonal tubes can be seen on the intervallum face of the inner wall, as in *E. rugosus* and *E. equivallum*.

Erismacoscinus petersi (R. & W. R. Bedford)

(Pl. 10, figs. 4 and 5)

1934 *Coscinocyathus petersi* R. & W. R. Bedford : 3, pl. 3, fig. 13.

HOLOTYPE. B.M. (N.H.) S 4158.

DESCRIPTION. The holotype is a unique, small, well-preserved specimen. The outer wall is simply porous with prominent, sharply-ridged, vertical crests between the septa. The inner wall is a skeletal plate that is perforated by vertical and horizontal rows of regular pores. Consequently, the wall tissue between neighbouring horizontal rows of pores, forms a continuous circular bar. A small tongue-like plate arises from the bar under each pore, but it was not possible to discover whether these tongues are separate from each other, or connected to form an annular ring. The radial septa have scattered regular pores, while the tabulae consist of a thin porous net.

DIMENSIONS

	(mm.)
Cup:	
Height	9
Diameter	9
Intervallum	1·51
Interseptum (outer wall)	0·83
(inner wall)	0·56
Intervallum coefficient	0·25
Parietal coefficient	2
Outer wall:	
8 pores (4+4) per interseptum	..
Diameter of pores	0·07
Thickness of linteaux	0·07
Thickness of wall	0·11
Inner wall:	
No. of rows of pores per interseptum	2
Diameter of pores	0·07
Vertical partitions	0·11
Horizontal partitions	0·07
Thickness of wall	0·26
Septa:	
No. of rows of pores per septa	6
Diameter of pores	0·03
Vertical partitions	0·11
Horizontal partitions	0·11–0·26
Tabulae:	
No. of rows of pores per interseptum	12
Diameter of pores	0·03
Partitions	0·11

DISCUSSION. The horizontal alignment of the inner wall pores is an important feature, that is a precursor to the formation of annular structures. This is evident in this case, for the horizontal bars are already slightly modified by supplementary plates. However, as the stage of a single pore per interseptum has not been reached, this species should be retained in *Erismacoscinus* and not placed in a genus of the Salairocyathidae. The star-shaped form of the external wall is similar to that of *E. cancellatus* (Bornemann), but the two species have no other features in common.

Erismacoscinus retifer (R. & W. R. Bedford)

(Pl. 10, figs. 2 and 3)

1934 *Coscinocyathus retifer* R. & W. R. Bedford : 3, pl. 3, fig. 14.
1964 *Erismacoscinus retifer* (R. & W. R. Bedford) Debrenne : 167.

HOLOTYPE. B.M. (N.H.) S 4159.

DESCRIPTION. The species is based on a single, small, incomplete specimen, but it is sufficiently well-preserved to enable one to see the details of each skeletal plate. The thin outer wall is perforated by 4–5 vertical rows of pores to each interseptum, these pores also form horizontal rows. The septa and the only visible tabula are of the same thickness as the outer wall, and have their round pores arranged in quincunx; the skeletal tissue between them is wider than the pores and projects slightly.

The inner wall is thicker than the other plates. The pores are elliptical, with the larger diameter horizontal and a tongue arising under each pore. One vertical row of pores is only just separated from the next and, at times, pores from neighbouring rows may join, giving a single pore at that point of the interseptum. At certain places, the pores are aligned horizontally and this involves two sporadic modifications. Firstly, the coalescence of two neighbouring pores, which predicts the uniserially-pored inner wall. Secondly, the development of small tongue-like plates under the pores, forecasting the formation of annular plates.

DIMENSIONS

	(mm.)
Cup:	
Height (*pars*)	9
Diameter	8
Intervallum	1·96
Intervallum coefficient	0·5
Parietal coefficient	3·5
Outer wall:	
No. of pore rows per interseptum	4–5
Diameter of pores	0·07
Vertical partitions	0·10
Horizontal partitions	0·10
Thickness	0·13
Inner wall:	
Diameter of pores	0·28–0·18
Vertical partitions	0·10
Horizontal partitions	0·15
Length of plates	0·20
Septa:	
No. of pores per loculus	9–10
Diameter of pores	0·11
Distance between horizontal rows	0·18
Distance between vertical rows	0.22
Tabulae:	
No. of pores per interseptum	6
Diameter	0·04
Partitions	0·05
Thickness	0·05

DISCUSSION. This species continues to follow the evolution already outlined under *E. petersi* and heralds the annular forms of Salairocyathidae.

Family **POLYCOSCINIDAE** Debrenne, 1964

Diagnosis. Cup with porous septa and tabulae. Double, porous outer wall. Simple inner wall.

Composition of the Family. *Polycoscinus* R. & J. Bedford 1937, *Tomocyathus* Rozanov 1960

Genus ***TOMOCYATHUS*** Rozanov, 1960

1960 *Tomocyathus* Rozanov : 664, figs. 1 d, e.
1964 *Tomocyathus* Rozanov; Debrenne : 115
1964 *Tomocyathus* Rozanov; Repina *et al.* : 231.
1965 *Tomocyathus* Rozanov; Hill : 107

Type Species. *Tomocyathus operosus* Rozanov 1960, by original designation.

Diagnosis. Outer wall coarsely porous, covered by a secondary micro-porous sheath. Straight septa and convex tabulae, both with numerous fine pores. Vesicular tissue. Inner wall with simple pores, and stellate in transverse section.

Discussion. The fluting of the walls is often considered a character of subgeneric value (Krasnopeeva 1955; Debrenne 1964). Recently, Repina *et al* (1964 : 231) described *Tomocyathus* without any mention of the stellate inner wall. Some species that they included in this genus, *compositus* (Zhuravleva) and *shoriensis* Rozanov, have little to no vesicular tissue, rather flat tabulae and the inner wall is not fluted but possesses spines of varying size and shape.

According to criteria used in distinguishing other subgenera e.g. *Ajacicyathus* (*Urcyathus*) Vologdin, one must create a new subgenus for the smooth forms of *Tomocyathus*.

Composition of the Genus. *Tomocyathus* (*Tomocyathus*) *operosus* Rozanov 1960, *T.* (*Tomocyathus*) *michniaki* Rozanov 1966; for subgenus *Tomocyathus* (*Erugatocyathus*) see below.

Subgenus ***ERUGATOCYATHUS*** nov.

Derivation. *erugatus* = unfolded.

Type Species. *Coscinocyathus papillatus* R. & W. R. Bedford, designated here.

Diagnosis. *Tomocyathus* with non-folded inner wall.

Composition of the Subgenus. *Tomocyathus* (*Erugatocyathus*) *echinus* (Debrenne 1964), *T.* (*E.*) *compositus* Zhuravleva 1955, *T.* (*E.*) *gini* Missarzhevsky & Rozanov 1962, *T.* (*E.*) *kundatus* Rozanov 1966, *T.* (*E.*) *shoriensis* Rozanov 1964, *T.* (*E.*) *papillatus* (R. & W. R. Bedford 1934).

Tomocyathus* (*Erugatocyathus*) *papillatus (R. & W. R. Bedford)

(Pl. 11, fig. 2, Text-fig. 9)

1934 *Coscinocyathus papillatus* R. & W. R. Bedford : 3, pl. 3, fig. 12.
1964 *Erismacoscinus papillatus* (R. & W. R. Bedford) Debrenne : 167

Holotype. B.M. (N.H.) S 4153.

Paratype. B.M. (N.H.) S 4154.

DESCRIPTION. Fragments of cylindrico-conical fossils. Septa with remote round pores. Tabulae reticular. Loculi rectangular and irregular in size. The circular pores at the base of the coarsely-porous outer wall are covered by a microporous sheath, in which each group of micropores consists of a central pore surrounded by five others.

A skeletal tongue covers each simple pore of the inner wall, it arises under the pore, curves upwards and rejoins the wall above. As the rows of pores alternate, each pore is surrounded by 4 knobs, corresponding to the beginning of a papilla. This feature is well shown in the weathered specimen S 4154 (see Text-fig. 9).

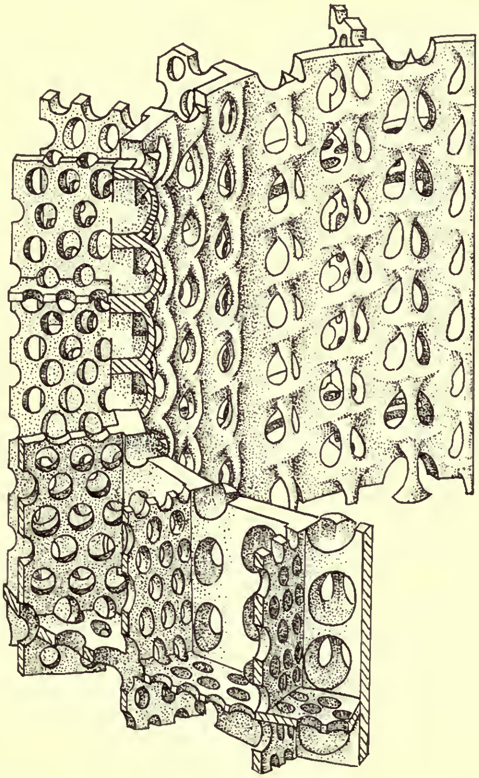

FIG. 9. *Tomocyathus* (*Erugatocyathus*) *papillatus* (R. & W. R. Bedford)

DIMENSIONS

	S 4153 Upper (mm.)	S 4153 Lower (mm.)	S 4154 (mm.)
Cup:			
Height	20		18
Diameter	13	8	10·5
Intervallum coefficient	1·89	1·5	..
Parietal coefficient	3·8	..	..
Intervallum	0·40	0·34	0·41
Interseptum	..	..	2·5–4

DIMENSIONS—*continued*

	S 4153 Upper (mm.)	S4153 Lower (mm.)	S 4154 (mm.)
Outer wall:			
No. of rows of pores per interseptum	..	2	2
Diameter	0·15	0·15–0·03	0·18
Vertical skeletal partitions	0·15–0·18	0·15–0·03	0·15
Horizontal skeletal partitions	..	0·15–0·03	0·15
Thickness	0·15	0·11	..
Inner wall:			
No. of pore rows per interseptum	2	2	2
Diameter	0·22	0·20	0·20
Vertical skeletal partitions	0·15	..	..
Horizontal skeletal partitions	0·15	..	..
Thickness	0·10+pap. = 0·11	0·22	..
Septa:			
No. of pore rows per intervallum	10	8	..
Diameter	0·05	0·07	0·07
Vertical skeletal partitions	0·10	0·11	0·11
Horizontal skeletal partitions	..	..	0·11
Thickness	0·07	0·07	0·07
Tabulae			
No. of pore rows per interseptum	5–6	4–5	4
Diameter	0·05	0·05	0·07
Vertical skeletal partitions	0·07	0·05	0·07
Thickness	0·05	0·05	0·05

DISCUSSION. These peculiar curved tongues are not known in any other species of the Regularia.

Family **SALAIROCYATHIDAE** Zhuravleva, 1955

DIAGNOSIS. Cups with intervallum crossed by porous septa and tabulae. Simple outer wall, but annular inner wall.

COMPOSITION OF THE FAMILY. *Salairocyathus* (*Salairocyathus*) Vologdin 1940, *Salairocyathus* (*Polystillicidocyathus*) Debrenne 1959.

Genus ***SALAIROCYATHUS*** Vologdin, 1940

1940a *Salairocyathus* Vologdin : 89

TYPE SPECIES. *Salairocyathus zenkovae* Vologdin 1940: 89, pl. 26, fig. 6.

DIAGNOSIS. Simple pores in outer wall and also in septa and tabulae. Annuli on inner wall, v-shaped in section and open towards the top.

COMPOSITION OF THE GENUS. *Salairocyathus* (*Salairocyathus*) *zenkovae* Vologdin 1940, *S.* (*S.*) *pospelovi* Zhuravleva 1960, ? *S.* (*S.*) *annulatus* (R. & W. R. Bedford 1934). *Salairocyathus* (*Polystillicidocyathus*) *erbosimilis* Debrenne 1959.

? ***Salairocyathus* (*Salairocyathus*) *annulatus*** (R. & W. R. Bedford)

(Pl. 11, fig. 4, Text-fig. 10)

1934 *Coscinocyathus annulatus* R. & W. R. Bedford : 4, pl. 3, fig. 17.

HOLOTYPE. S 4163 in British Museum (Natural History).

DESCRIPTION. A unique, very fragmentary specimen, that has part of the inner wall, as seen from the central cavity, well preserved. Porous outer wall, but not possible to distinguish their arrangement. Septa and tabulae frame somewhat parallelepipedic loculi. The rectangular openings of the inner wall are bounded by the inner edges of the septa and a vertical series of horizontal bars, which are annular in form. The β component of the latter is thick and horizontal, while the α component is much thinner and curves backwards up to the middle of the following horizontal row of openings, which are thus partly closed, (see Text-fig. 10).

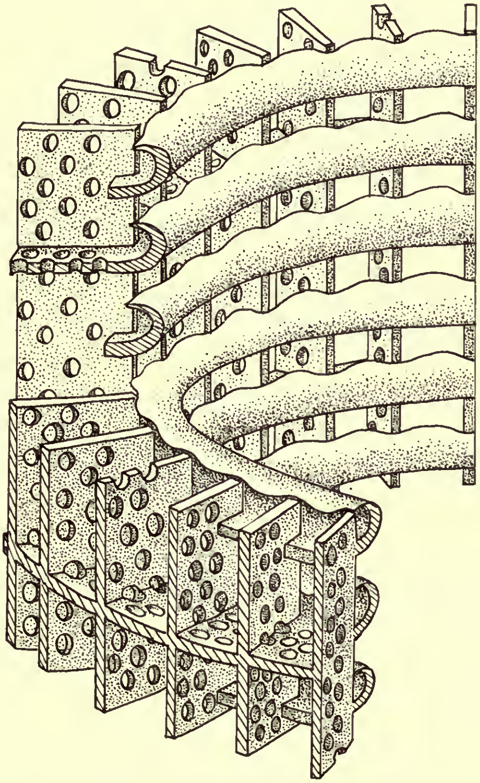

FIG. 10. *Salairocyathus* (*Salairocyathus*) *annulatus* (R. & W. R. Bedford)

DIMENSIONS

	(mm.)
Cup:	
Height	27
Diameter	11
Intervallum	?
Interseptum	0·22–0·30
Intertabulum	about 1·35
Outer wall:	
No. of rows of pores per interseptum	probably 4
Thickness	0·13
Inner wall:	
No. of rows of pores per interseptum	1
Diameter of pores (lengthened horizontally)	0·25–0·15
Skeletal partitions (constant thickness)	0·06
Septum:	
Diameter of pores	0·06
Skeletal partitions	0·13
Thickness	0·13
Tabulae:	
Diameter of pores (radially lengthened)	0·13–0·06
Skeletal partitions	0·06
Thickness	0·15

DISCUSSION. This annular form of inner wall was previously unknown. The specimen is described as *Salairocyathus* with reservation.

Family **ALATAUCYATHIDAE** Zhuravleva, 1955

DIAGNOSIS. Cups with simply porous septa and tabulae. Inner wall with simple, or S-shaped pores. Two sub-families are distinguished by the shape of the pores in the outer wall.

Subfamily **TUMULOCOSCININAE** Zhuravleva, 1960

DIAGNOSIS. Outer wall with simple tumuli.

COMPOSITION OF THE SUBFAMILY. *Tumulocoscinus* Zhuravleva 1960, *Ethmocoscinus* Simon 1939, *Asterotumulus* Rozanov 1964.

Subfamily **ALATAUCYATHINAE** Zhuravleva, 1960

DIAGNOSIS. Outer wall with knobbly tumular pores.

COMPOSITION OF THE SUBFAMILY. *Alataucyathus* (*Alataucyathus*) Zhuravleva 1955, *Alataucyathus* (*Anaptyctocyathus*) subgen. nov.

Subfamily **TUMULICOSCININAE** Zhuravleva, 1960

Genus ***ETHMOCOSCINUS*** Simon 1939

1939 *Ethmocoscinus* Simon : 28

TYPE SPECIES. *Coscinocyathus papillipora* R. & W. R. Bedford, by original designation (Simon 1939 : 28).

DIAGNOSIS. Cylindro-conical cups. Outer wall with simple tumuli, one per interseptum. Inner wall with a single row of S-shaped pore-tubes per interseptum. Septa have sparse simple pores. Tabulae with polygonal, somewhat irregular pores.

COMPOSITION OF THE GENUS. A single species *E. papillipora* (R. & W. R. Bedford).

Ethmocoscinus papillipora (R. & W. R. Bedford)

(Pl. 3, fig. 3)

1934 *Coscinocyathus papillipora* R. & W. R. Bedford : 18.
1939 *Ethmocoscinus papillipora* (R. & W. R. Bedford) Simon : 28.

HOLOTYPE. B.M. (N.H.) S 4164.

DESCRIPTION. The holotype, the only known specimen, is partly weathered-out and shows the structure of the two walls. The straight septa are perforated by round regular pores, which although few, are arranged in quincunx. A single tabula is visible (it is therefore impossible to state the frequency) and consists of a net of regular pores. The papillae of the outer wall are situated between the septa in vertical rows, which are just separate from one interseptum to the next. The papillae of the inner wall occupy a much larger area and also appear to be in alternate vertical rows.

DIMENSIONS

Cup:	(mm.)
Height (pars)	20
Diameter	7·5
Intervallum	1·2
Interseptum	from 0·41–0·45
Number of septa	26
Parietal coefficient	3·4
Intervallum coefficient	0·2
Outer wall:	
No. of pore rows per intersept	1
No. of pore rows before formation of septa	2
Diameter of papilla	0·34–0·22
Thickness of papilla	0·07
Height of papilla	0·18
Horizontal partitions	0·15–0·18
Vertical partitions	0·11
Inner wall:	
No. of rows of pores per interseptum	1
Diameter of pores	0·37
Partitions	0·11
Septa:	
No. of rows of pores per intervallum	4
Diameter of pores	0·11
Partitions	0·11
Thickness	0·06
Tabula:	
No. of rows of pores per interseptum	6
Diameter of pores	0·07
Partitions	0·03
Thickness	0·03

Subfamily **ALATAUCYATHINAE** Zhuravleva, 1960

Genus ***ALATAUCYATHUS*** Zhuravleva, 1955

1955 *Alataucyathus* Zhuravleva : 626, figs. 1a, 2d.

Type Species. By original designation *Alataucyathus jaroschevitschi* Zhuravleva 1955 : 626.

Diagnosis. Intervallum filled with simple septa and tabulae. Outer wall covered with small multi-perforate knobs. Inner wall simple with vertical folds between neighbouring septa.

Discussion. As mentioned in the discussion on *Tomocyathus*, it is considered that species having non-fluted inner walls, should be placed in a separate sub-genus.

Subgenus ***ALATAUCYATHUS*** (***ANAPTYCTOCYATHUS***) nov.

Derivation. *anaptyctos* = unfolded.

Type Species. *Coscinocyathus cribripora* R. & W. R. Bedford designated here.

Composition of the genus. *A.* (*A.*) *cribripora* (R. & W. R. Bedford, 1934), *A.* (*A.*) *minimiporus* (R. & J. Bedford 1937)—included with some doubt as the structure of the walls is not certain, *A.* (*A.*) *excellenthis* (Rozanov 1964), *A.* (*A.*) *verschkhovskajae* (Zhuravleva 1961), and *A.* (*A.*) *flabellus* nov.

Alataucyathus (***Anaptyctocyathus***) ***cribripora*** (R. & W. R. Bedford)

(Pl. 11, figs. 1 and 3)

1934 *Coscinocyathus cribripora* R. & W. R. Bedford : 3, pl. 3, fig. 15.

Holotype. B.M. (N.H.) S 4160.

Description. Cylindrical cup. Intervallum with straight radial septa, in which the hexagonal pores occupy a much larger surface in proportion to the skeletal tissue, and irregularly distributed flat tabulae, that are finely perforated by very narrow pores.

The inner wall is simple, with two rows of pores per interseptum, which are only weakly separated, in fact, towards the upper part of the cup, two neighbouring pores may sometimes coalesce. The pores of the outer wall are covered by knobs, that are perforated by a central pore and a surrounding circle of six others.

Dimensions

	(mm.)
Cup:	
Height (*pars*)	36
Upper diameter	12
Lower diameter	6
Intervallum coefficient	0·28
Interseptum (Upper diameter)	0·74
(Lower diameter)	0·56
Intertabula	2–5

DIMENSIONS—*continued*

	(mm.)
Outer wall:	
No. of rows of main pores per interseptum (each pore covered by a sheath with 7 micropores)	2
Main pore diameter	0·27
skeletal partitions	0·27–0·30
Micropore diameter	0·07
skeletal partitions	0·03
Inner wall:	
No. of pore rows per interseptum	2 (these sometimes coalesce)
Diameter of pores	0·30
Skeletal partitions	0·07
Septa:	
No. of hexagonal pores	4–5
Diameter	0·15–0·18
Vertical partitions	0·18
Horizontal partitions	0·18
Tabulae:	
No. of pores	10–4
Diameter	0·11–0·06
Partitions	0·07

DISCUSSION. *A.* (*A.*) *cribripora* differs from the two Russian species by having lower tumuli, coarse micropores and a thicker inner wall.

Alataucyathus* (*Anaptyctocyathus*) *flabellus nov.

(Pl. 10, fig. 1)

HOLOTYPE. B.M. (N.H.) S 4161.

DESCRIPTION. Bowl-shaped cup with narrow intervallum. Regularly porous septa in alternate vertical rows. The tabulae almost join, their pores are much thinner than those of the septa. The inner wall is only known from the intervallum side and therefore, it is not possible to discover whether there are spines on the central cavity face. Three vertical rows of pores can be distinguished per interseptum. The outer wall has 2–3 pores, each covered by a small microporous tumulus with about ten angular pores in each.

DIMENSIONS

	(mm.)
Cup:	
Height (*pars*)	20
Span of visible arc	78
Intervallum	2
Loculi	1/ 2/ 3
Outer wall:	
No. of rows of pores per interseptum	from 2–3
Diameter of main pores	0·40–0·27

DIMENSIONS—*continued*

	(mm.)
Vertical skeletal partition	0·16
Horizontal skeletal partition	0·11
Diameter of micropores	0·06
Skeletal partition between micropores	0·03
Inner wall:	
Diameter of pores	0·18
Skeletal partitions	0·22
Thickness	**0·20**
Septa:	
Diameter of pores	0·20
Vertical partitions	0·30
Horizontal partitions	0·20
Thickness	0·11
Tabulae:	
No. of rows of pores per interseptum	5
Diameter of pores	0·06
Skeletal partitions	0·06
Thickness	0·11

DISCUSSION. Differs from *A.* (*A.*) *cribripora* by its bowl-shaped cup, the specific coefficients and the different arrangement of the outer wall pores.

Class *IRREGULARIA* Vologdin, 1937

Order ARCHAEOCYATHA Okulitch, 1935

Family **DICTYOCYATHIDAE** Taylor, 1910

DIAGNOSIS. Cups with intervallum containing disorientated short rods and dissepiments. Two simply porous walls.

COMPOSITION OF THE FAMILY. *Dictyocyathus* Bornemann 1891, *Spinosocyathus* Zhuravleva 1960, *Pinacocyathus* R. & W. R. Bedford 1934, *Agastrocyathus* Debrenne 1964, *Archaeopharetra* R. & W. R. Bedford 1936, *Chouberticyathus* Debrenne 1964.

Genus ***PINACOCYATHUS*** R. & W. R. Bedford, 1934

1934 *Pinacocyathus* R. & W. R. Bedford : 4, fig. 21.
1964 *Pinacocyathus* R. & W. R. Bedford; Debrenne : 200
1965 *Pinacocyathus* R. & W. R. Bedford; Hill : 117, fig. 22, 7a and b.

TYPE SPECIES. By monotypy *Pinacocyathus spicularis* R. & W. R. Bedford 1934 : 4.

DIAGNOSIS. Two-walled cup with intervallar rods. The outer wall is formed by a scaffolding of vertical pillars connected by horizontal, or slightly oblique rods. The inner wall is, probably, a regular net. Oblique, or radial horizontal rods in the intervallum.

COMPOSITION OF THE GENUS. A single species; *P. spicularis*.

Pinacocyathus spicularis R. & W. R. Bedford

(Pl. 12, figs. 1, 2, Text-fig. 11)

1934 *Pinacocyathus spicularis* R. & W. R. Bedford : 4, fig. 21.

Holotype. By monotypy B.M. (N.H.) S 4169.

Description. Conical tube. The outer wall consists of an open framework, which is mainly composed of vertical columns arranged around the cup at almost regular intervals. This framework is completed by horizontal, or oblique rods, which connect the columns, with a few spines occurring at the junctions. On the lower part, the net is more compact but hidden by poor preservation, that has swollen the structures. Only one vertical row of the inner wall can be seen and this seems to be composed of a regular mesh. However, it was not possible to determine the arrangement of the intervallar rods. They seem to arise from the skeletal junctions of the outer wall framework and continue radially, or obliquely towards the inner wall. The framework is probably thicker in its lower parts.

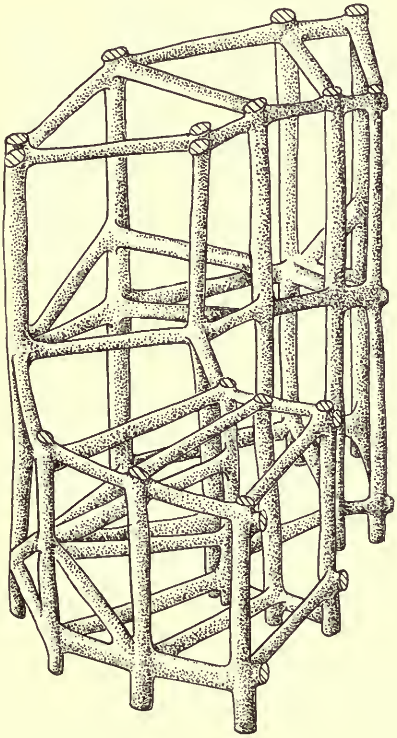

Fig. 11. *Pinacocyathus spicularis* R. & W. R. Bedford

DIMENSIONS

	(mm.)
Cup:	
Height (*pars*)	15
Diameter	5·75
Intervallum	1·42
Central cavity	0·6
Outer wall:	
Diameter of pores	0·55
Distance between vertical rods	0·67–1·0
Distance between horizontal rods	1·35–1·70
Thickness of vertical rods	0·33
Thickness of horizontal rods	0·33
Thickness of oblique rods	0·25
Inner wall:	
Diameter of pores	0·33
Vertical partitions	0·20
Horizontal partitions	0·20
Thickness	0·20
Intervallar rods:	
Thickness	0·27

DISCUSSION. Only one specimen of this curious form is known. It is included in the Dictyocyathidae because of its scaffolding of intervallar rods, but no other recognized genus has such a loosely-spaced framework.

Family **FLINDERSICYATHIDAE** R. & J. Bedford, 1939

DIAGNOSIS. Two-walled cups, simply porous, with a single series of large pores in the inner wall. A scaffolding of rods fills the intervallum, consisting of taeniae, that cross the intervallum, joining the septa, and undulate in a radial plane, together with synapticulae, which connect the crests of neighbouring taeniae. Little to no vesicular tissue is present. Apex of *Dictyocyathus*-type.

COMPOSITION OF THE FAMILY. *Spirocyathella* Vologdin 1939, *Flindersicyathus* (*Flindersicyathus*) R. & J. Bedford 1937, *Flindersicyathus* (*Pycnoidocyathus*) (Taylor 1910), ? *Spirillicyathus* R. & J. Bedford, 1937, *Copleicyathus* R. & J. Bedford 1937.

Genus ***FLINDERSICYATHUS*** R. & J. Bedford, 1937

1910 *Pycnoidocyathus* Taylor : 131.
1937 *Flindersicyathus* R. & J. Bedford : 28.
1939 *Flindersicyathus* R. & J. Bedford; Simon : 30.
1960 *Archaeocyathus* Billings; Zhuravleva : 296 (*pars*).
1965 *Flindersicyathus* R. & J. Bedford; Hill : 123.

TYPE SPECIES. *Flindersicyathus decipiens* R. & J. Bedford, by subsequent designation R. & J. Bedford (1939(May) : 78), which has priority over *Spirocyathus irregularis* Taylor chosen by Simon (1939 (Dec.) : 30), see Hill (1965 : 123). Holotype material No. 86670 in Princeton University, U.S.A.

DIAGNOSIS. Hill (1965 : 123) writes: " solitary cups, with simply porous outer wall; inner wall with a single series of large rounded pores per intertaenial loculus, each pore bounded by the taeniae and the synapticulae joining them, and each with a louvre-like plate projecting upwards and inwards to the central cavity from its low synapticula". [In fact, each pore is a short tube with the lower part projecting into the central cavity, rather than a simple pore with a projecting plate.] Intervallum with taeniae, sparsely porous near the inner wall, coarsely and copiously porous elsewhere; the taeniae are waved in the radial plane, and the waves have angulated crests and troughs, the crests and the trough-lines curving upwards and outwards from the inner wall; the crests of neighbouring taeniae are opposed and connected by synapticulae. Rare dissepiments may occur. No tabulae ".

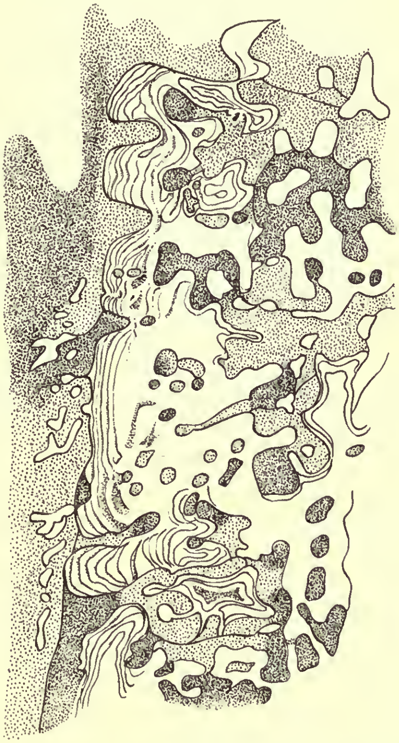

FIG. 12. *Archaeocyathus atlanticus* Billings × 4

DISCUSSION. R. & J. Bedford (1937 : 28) and Hill (1965 : 123 and 128) point out that *Flindersicyathus* R. & J. Bedford and *Pycnoidocyathus* Taylor have a very similar structure. The latter differs only in having much stronger transverse annulations of the intervallum, the inner wall of both remaining cylindrical. The two genera may be synonymous, but I have not seen examples of the type species of *Flindersicyathus*, or the type material of *Pycnoidocyathus* and therefore cannot settle the question. My tentative suggestion is that *Pycnoidocyathus* should be considered a subgenus of *Flindersicyathus*, due to its different outer shape, although possibly having a similar structure. This situation is comparable to the distinction between *Ajacicyathus* R. &

J. Bedford and *Orbicyathus* Vologdin, which are considered to be subgenera distinguished by their external shape.

Zhuravleva (1960 : 296) placed *Flindersicyathus* in synonymy with *Archaeocyathus* Billings 1861. Debrenne (1964 : 117) doubtfully placed *Flindersicyathus* in the family Archaeocyathidae (as did Hill 1965 : 123), but had maintained its independence. However, having seen the holotype of *Archaeocyathus atlanticus* Billings (1861, fig. 10). I can state that the taeniae are thickened by several skeletal layers, have few and irregular pores (Text-fig. 12), are goffered longitudinally and transversely, and are occasionally connected to the opposite crests, more or less forming elongated pores. The curved hexagonal tubular mesh of *Flindersicyathus* was not recognized. Further characters which separate the two genera are the abundant vesicular tissue, the pore canals of the inner wall and the irregular net of the outer wall of *Archaeocyathus*.

Composition of the Genus. *Flindersicyathus* (*Flindersicyathus*): *F. decipiens* R. & J. Bedford, 1937, *F. circliporus* R. & J. Bedford, 1937, *F. contractus* Hill 1965, *F. graphicus* (R. & W. R. Bedford 1934), *F. irregularis* (Taylor 1910), *F. latiloculatus* Hill 1965, *F. major* (R. & W. R. Bedford 1934), *F. multifidus* (R. & W. R. Bedford 1936), ? *F. macdonnelli* R. & J. Bedford 1937, *F. rete* (R. & W. R. Bedford 1936), *F. simplex* (Taylor 1910), *F. speciosus* (R. & W. R. Bedford 1934), *F. tabulatus* R. & J. Bedford 1937.

Flindersicyathus (*Pycnoidocyathus*): *F. synapticulosus* (Taylor 1910), *F. maximipora* (R. & W. R. Bedford 1936), *F. parvulus* (R. & W. R. Bedford 1936), *F. ptychophragma* (Taylor 1910), *F. vicinisepta* (R. & W. R. Bedford 1936).

Flindersicyathus* (*Flindersicyathus*) *graphicus (R. & W. R. Bedford)

(Pl. 12, figs. 3–5, Text-fig. 13)

1934 *Protopharetra graphica* R. & W. R. Bedford : 4, pl. 4, fig. 22.
1939 *Dictyocyathus graphicus* (R. & W. R. Bedford) R. & J. Bedford : 73.
1964 *Metaldetes graphica* (R. & W. R. Bedford) Debrenne : 220.

Holotype. B.M. (N.H.). S 4170.

Paratypes. B.M. (N.H.) S 4171–4173.

Other Material. B.M. (N.H.) S 4761, S 7629.

Description. Slender conical cups, undulating exterior form, with the bulges of the inner wall following those of the outer wall, so that the intervallum remains a constant width. Thin outer wall, perforated by hexagonal to ellipsoidal pores, recalling the outer wall of the Regularia. There is no specific inner wall, but, instead, the innermost face is formed by the inner edges of the taeniae and connecting bars, which enclose apertures that are, in effect, " wall pores ".

The structure of the intervallum can, perhaps be considered as an assemblage of septa of the *Volvacyathus*-type, with regular, somewhat rounded, hexagonal pores set in a radial plane, with the line of pores curving upwards and outwards from the inner to the outer wall. These pseudo-septa (flat taeniae) are joined to one another by horizontal synapticulae and join the skeleton at each pore angle. No vesicular tissue. Early stages of the species unknown.

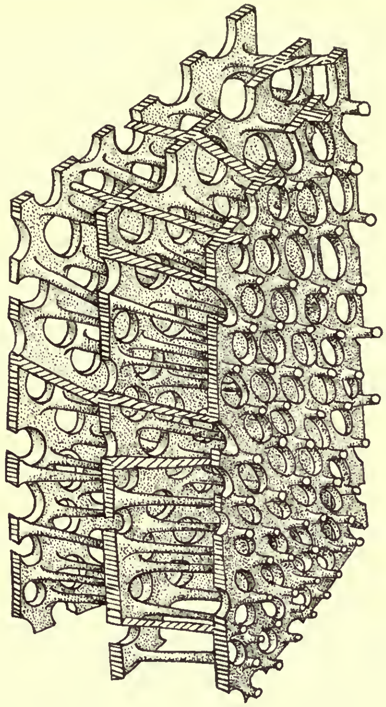

FIG. 13. *Flindersicyathus* (*Flindersicyathus*) *graphicus* (R. & W. R. Bedford)

Dimensions

	S 4170 (mm.)	S 4171 (mm.)	S 4172 (mm.)	S 4173 sup. (mm.)	S 4173 inf. (mm.)	S 7629 (mm.)	S 4761 (mm.)
Cup:							
Height	35	45	15	..	..	45	30
Diameter	12	14	15	7	4	20	18
Intervallum	1·9	1·7	2	1·5	1·13	1·5	1·5
Intervallum coefficient	0·25	0·17	0·18	0·3	0·6	0·1	0·1
Bars:							
Radial distance	0·26	0·18	0·34	0·15	0·15	0·37	0·22
Tangential distance	0·26	0·26	0·41	0·22	0·30	0·30	0·22
Vertical distance	0·37	0·26	0·37	..	..	0·36	0·22
Thickness	0·07	0·07	0·07	0·07	0·07	0·07	0·07
Outer wall:							
No. of pores per intertaeniae	3	3	..	..	..	3	3
Diameter of pores	0·11–0·09	0·07	..	..	..	0·11	0·11
Partitions	0·03	0·03	..	..	..	0·05	0·07
Thickness	0·11	0·07	0·11	0·05	..	0·07	0·07
Inner wall:							
No. of pores per intertaeniae	1	1	..	1	..	..	..
Diameter of pores	0·26	0·22	0·37	0·18	..	0·18	0·18
Partitions	0·13	0·07	0·15	0·07	..	0·11	0·11
Thickness	0·18	0·11	..	0·11	0·07	..	..

Discussion. The taeniae (pseudosepta) of *graphicus* are not waved in the radial plane, as has been described in *F. decipiens* (R. & J. Bedford) probably because of the narrowness of the intervallum and the density of the taeniae and synapticulae. The inner wall does not have a plate on the lower part of the pore. Thus *graphicus* is much simpler than other species of *Flindersicyathus*, but the presence of well defined radial plates (flat taeniae) indicates a more complex stage than that of having sparse rods or plaquettes.

The species was first described as *Protopharetra*, subsequently as *Dictyocyathus* and then, in 1964, removed to *Metaldetes* because of the pseudosepta. However, it differs from *Metaldetes* in having a very regular outer wall, numerous synapticulae and the absence of connections between these. The scaffolding of the intervallar mesh is very like that of *Tabellaecyathus* Fonin but the walls are simpler, neither tabello-reticulate nor tabello-porous.

Flindersicyathus* (*Flindersicyathus*) *irregularis (Taylor)

(Pl. 14, fig. 4)

1910 *Spirocyathus irregularis* Taylor : 148, pl. 16, figs. 93–94.
1936 *Spirocyathus irregularis* Taylor; R. & W. R. Bedford : 14, pl. 13, fig. 64.
1937 *Flindersicyathus irregularis* (Taylor) R. & J. Bedford : 28.
1937 *Spirocyathus atlanticus* Billings; Ting : 368–369, pl. 13, fig. 14.
1961 *Archaeocyathus irregularis* (Taylor) F. & M. Debrenne : 702, pl. 20, fig. 5.

Material. B.M. (N.H.) S 7625, S 4763.

Description. Two-walled cup with numerous thin radial taeniae, probably quite porous [a deduction made from Taylor's comparison with *F. rete* in his original description of *F. irregularis* and not from observation, as no specimen showing a longitudinal section was available], wavy and connected by synapticulae which form a network of more or less regular polygonal apertures, particularly in the outer part. Vesicular tissue sparse. Skeletal tissue is sometimes thickened by secondary layers and occurs mainly near the inner wall (see Pl. 14, fig. 4; also F. & M. Debrenne, 1961, pl. 20, fig. 5). Thin outer wall, with numerous small pores; inner wall with one vertical row of pores per intertaenial space.

Dimensions

	Taylor (mm.)	Ting (mm.)	S 7625 (mm.)	S 4763 (mm.)
Cup:				
Height (*pars*)	50	17	16	25
Diameter	14	16·5	18	20
Intervallum coefficient	0·5	0·8	0·8	0·9
Intertaenial space	0·5	0·4	0·45	0·5
Intersynapticular space				
Horizontal	..	..	0·70	0·6
Vertical	..	..	irregular	..
Taeniae thickness	0·1	0·12	0·2	0·2

DIMENSIONS—*continued*

	Taylor (mm.)	Ting (mm.)	S 7625 (mm.)	S 4763 (mm.)
Outer wall:				
Diameter of pores	..	0·2–0·4	..	..
Partitions	..	0·12	..	..
Thickness	..	0·12	0·13	0·15
Inner wall:				
Diameter of pores	..	0·5	0·35	0·33
Partitions	..	0·3	0·27	0·3
Thickness	..	1	1	1

DISCUSSION. The taeniae are thinner and more numerous than in other species of *Flindersicyathus*, and the thickening of the inner wall recalls some transverse sections of *Copleicyathus confertus* R. & J. Bedford (Hill 1965: pl. 10, figs. 4a–b), but at the moment, it is not possible to take the comparison any further.

Flindersicyathus* (*Flindersicyathus*) *major (R. & W. R. Bedford)

(Pl. 14, fig. 2)

1934 *Spirocyathus major* R. & W. R. Bedford : 5, pl. 4, fig. 24.

HOLOTYPE. B.M. (N.H.) S 4174.

DESCRIPTION. Only one broken specimen known. The outer wall is obscured by silicification. The inner wall has round, shaft-like pore tubes, that are limited by neighbouring taeniae and successive vertical synapticulae; the lower part of each tube is inclined downwards into the intervallum and projects slightly into the central cavity, whereas the upper part is flattened. The rows of pore-tubes alternate. The pores are more crowded at the base of the cup, because the taeniae are closer together there.

The intervallum is crossed by waved taeniae, with the crests and troughs of neighbouring taeniae opposite to one another. Abundant synapticulae join the taeniae, particularly in the central and outer parts of the intervallum. The ratio diameter of taenial pores: distance apart of the synapticulae is close to unity, so that the intervallum has the appearance of a tubular mesh with tubes curving upwards and outwards.

DIMENSIONS

	(mm.)
Cup:	
Height (*pars*)	40
Diameter	about 20
Intervallum	10
Interseptum	1·5
Outer wall:	
Thickness	0·20
Inner wall:	
Diameter of pores : horizontal	1·70
vertical	1·15
Horizontal partitions	1·15
Lateral partitions	0·33
Tubes:	
Irregular diameter	about 0·67
Large skeletal plates	
Thickness	0·27

Discussion. The septa are at wider intervals than in other species of *Flindersicyathus*.

Flindersicyathus* (*Flindersicyathus*) *speciosus (R. & W. R. Bedford)

(Pl. 14, figs. 1, 3)

1934 *Spirocyathus speciosus* R. & W. R. Bedford : 5, pl. 4, fig. 25.

Holotype. B.M. (N.H.) S 4175.

Description. Only a single broken specimen known. The taeniae are thin, radial, slightly waved and connected by sparse synapticulae, which are chiefly found in the outer part of the cup. The diameter of the taenial pores is less than the width of the skeletal tissue between them.

Outer wall with 4 to 5 alternating vertical rows of round pores per interseptum. The inner wall has a single tube per intertaenial space, the lower part of which projects into the central cavity, giving the tube a crescentic section. The rows alternate.

Dimensions

	(mm.)
Cup:	
Height (*pars*)	30
Upper diameter	about 13·5
Lower diameter	11
Intervallum	4·5
Intervallum coefficient	1
Intertaenial space; lower end of cup	0·6
upper part of cup	0·75
Outer wall:	
Diameter of pores	0·15
Vertical skeletal partitions	0·07
Horizontal skeletal partitions	0·18
Inner wall:	
Diameter of pores; horizontal	0·9
vertical	0·4
Vertical skeletal partitions	0·13
Crescentic plates	0·33

Discussion. The taeniae are less waved and not so distinct as those in *Flindersicyathus major*. The shaft-like tubes of the latter are not present, while the inner wall pores of *speciosus* are crescentic and very close together. Synapticulae are less numerous than in other *Flindersicyathus* species.

Subgenus ***FLINDERSICYATHUS* (*PYCNOIDOCYATHUS*)** (Taylor), 1910

1910 *Pycnoidocyathus* Taylor : 132.
1939 *Pycnoidocyathus* Taylor; R. & J. Bedford : 78.
1965 *Pycnoidocyathus* Taylor; Hill : 128

Type Species. *P. synapticulosus* Taylor (1910 : 132) by subsequent designation R. & J. Bedford, (1939 : 78); type material in the Univ. of Adelaide.

Discussion. Although Hill (1965 : 128) has provisionally treated this as a genus separate from *Flindersicyathus*, I regard it as a subgenus (see p. 345). It is very like *Flindersicyathus*, but with much stronger expansions and contractions of the intervallum which do not affect the inner wall. The problem can only be settled by examination of the type material, in order to discover whether dissepiments occur and the exact nature of the inner wall pores.

***Flindersicyathus* (*Pycnoidocyathus*) *synapticulosus* (Taylor)**

(Pl. 15, fig. 1)

1910 *Pycnoidocyathus synpaticulosus* Taylor : 132, pl. 12, fig. 69.
1936 *Pycnoidocyathus synapticulosus* Taylor; R. & W. R. Bedford : 15, pl. 15, fig. 69.

HOLOTYPE. Probably at Adelaide University.

MATERIAL. B.M. (N.H.) S 208, S 4825.

DESCRIPTION. Large cup with annular bulges. On the specimens examined here, the outer part of each bulge is made of successive flanges. Outer wall with somewhat irregular polygonal fine pores. Inner wall with a vertical series of short tubes per intertaenial space, the tubes lead upwards into the central cavity. Taeniae are radial, nearly flat and close together, particularly near the synapticulae, so that transverse sections appear to be composed of irregular polygonal cells. Abundant horizontal and vertical synapticulae; generally arranged in quincunx from one intersept to the next. It was not possible, to examine the size and arrangement of pores in tangential section, but Taylor's description (1910 : 132) and Bedford's figure (1936, fig. 69) confirm my observations from transverse sections which suggest the pores are small, isolated and without any important modifications in the lateral bulges. No vesicular tissue.

DIMENSIONS

	(mm.)
Cup:	
Diameter	about 85
Intervallum	
without bulges	8
largest part	19
Interseptum	1·07
Synapticulae	
horizontal	1–2
vertical	0·6–2
Outer wall:	
No. of pores per interseptum	4
Diameter of pores	0·13
Partitions	0·06
Inner wall:	
No. of pores per interseptum	1
Diameter of pores	0·33
Horizontal partitions	0·67
Thickness	0·67
Taeniae:	
Thickness	0·1

DISCUSSION. This is the largest species of *Flindersicyathus* (*Pycnoidocyathus*) known. It has regular annular bulges, the skeletal tissue of the wavy taeniae occupies a greater area than the pores, and the synapticulae are more numerous than in any other species of this genus.

Flindersicyathus* (*Pycnoidocyathus*) *simplex (Taylor)

(Pl. 15, fig. 2)

1910 *Pycnoidocyathus simplex* Taylor : 134, pl. 2, fig. 7c.
1936 *Pycnoidocyathus simplex* Taylor; R. & W. R. Bedford : 15, pl. 15, fig. 70.

HOLOTYPE. Probably in the South Australian Museum.

MATERIAL. B.M. (N.H.) S 4824.

DESCRIPTION. Broken piece showing well-preserved inner wall. Taeniae are radial, not waved and are joined with the synapticulae, chiefly towards the exterior. Outer wall is only see on part of a transverse section, where a small weathered-out surface shows that the pores are arranged in irregular quincunx. Inner wall has a vertical row of pores per intersept, each pore having a raised lower edge and is vertically elongated but flattens towards the top. The rows of pores alternate in quincunx.

DIMENSIONS

	(mm.)
Cup:	
Height (*pars*)	40
Diameter	about 22
Intervallum	5·5
Central cavity	13
Intervallum coefficient	0·4
Intertaenial space	1
Outer wall:	
Diameter of pores	0·40–0·33 (hor.)
Skeletal partitions	0·20–0·20
Thickness	0·13
Inner wall:	
Diameter of pores	1·69–1·42 (hor.)
Vertical partitions	0·20
Horizontal partitions	0·47
Taeniae:	
Diameter of pores	0·6
Vertical partitions	0·13
Horizontal partitions	0·20
Thickness	0·1

DISCUSSION. The measurements of the specimen described above correspond to those given by Taylor (1910). R. & W. R. Bedford (1936 : 15, fig. 70) pointed out and sketched the regular annular bulges from an example of the same species. *F.* (*P.*) *simplex* differs from typical *Pycnoidocyathus* by the scarcity of its synapticulae and the straight taeniae.

Flindersicyathus* (*Pycnoidocyathus*) *maximipora (R. & W. R. Bedford)

(Pl. 15, fig. 3)

1934 *Pycnoidocyathus maximipora* R. & W. R. Bedford : 3, pl. 2, figs. 9a–c.
1936 *Pycnoidocyathus maximipora* R. & W. R. Bedford : 15, pl. 15, fig. 71.

HOLOTYPE. B.M. (N.H.) S 4150.

Description. One broken specimen with a single annulate bulge. Intervallum crossed by un-waved radial, porous taeniae, with the skeletal tissue forming a greater area than the pores, and sparse synapticulae, that occur mainly in the lower part of the fragment. The taenial pores, are round and arranged in lines, which curve upwards and outwards, near the inner wall; but are oval and bigger near the outer wall and inside the annular bulge. The thin, irregular, outer wall is strengthened by bars springing from the taeniae, but both partial weathering and preservation give an irregular and false idea of its original structure.

The inner wall is composed of very short piled-up pipes, leading obliquely upward, with one row per intertaenial space, which alternates with the next. The cross-section of the pipe is vertically oval. Each pipe is withdrawn from the one immediately above and its sides are stretched slightly to join with its neighbours. Thus, the inner wall does not present a flat surface to the central cavity but has the appearance of a rasp. The various sections have suggested to previous authors that there is a louvre-like plate at the lower part of each pore, but, in fact, these are the short pipes.

Dimensions

	(mm.)
Cup:	
Height (*pars*)	35
Diameter	22
Intervallum	6
Intertaenial space	1·3
Outer wall:	
Diameter of the pores	0·4
Partitions	0·3
Thickness	0·4
Inner wall:	
Diameter of the pores	1·49–2·71
Lateral partitions	0·13
Horizontal partitions	2·03
Taeniae:	
Diameter of the pores near the inner wall	0·6
near the outer wall	0·8–2·35
Partitions	0·27–0·40

Discussion. This species differs from others by the greater development of tubes in the inner wall and its relatively narrower taenial pores.

Flindersicyathus (Pycnoidocyathus) vicinisepta (R. & W. R. Bedford)

(Pl. 15, fig. 4)

1936 *Pycnoidocyathus vicinisepta* R. & W. R. Bedford : 15, pl. 16, fig. 72.

Holotype. Probably in the South Australian Museum.

Material. B.M. (N.H.) S 4825.

Description. A longitudinally cut fragment. Several annulate horizontal bulges are visible, they are rather narrow and close together. Radial un-waved taeniae joined by numerous synapticulae. In the bulges, the taeniae are waved with opposite crests connected by synapticulae, so that the intervallum has the aspect of a polygonal mesh. A very small part of the outer wall is preserved in which the pores are irregular and polygonal. The inner wall has one vertical row of pore-tubes leading up into the central cavity, in each intertaenial space. The rows alternate.

DIMENSIONS

	(mm.)
Cup:	
Height (*pars*—in two pieces)	95
Diameter	22
Bulge	4
Intervallum without bulge	4
Central cavity	14
Intertaenial space	0·33
Intersynapticular space	0·47–0·67
Outer wall:	
Diameter of pores	0·06
Skeletal tissue	0·05
Thickness	not known
Inner wall:	
No. of rows of pores per intertaenial space	1
Horizontal partitions	0·27
Vertical partitions	0·40
Diameter of pores	0·40
Thickness	0·40
Taeniae:	
Diameter of pores	0·27
Horizontal partitions	0·81
Vertical partitions	0·67
Thickness	0·10

DISCUSSION. As far as I can tell, after measuring the drawings of Bedford, the coefficients correspond to those of *vicinisepta*. This species differs from other *Pycnoidocyathus* in having many more taeniae.

Family **METACYATHIDAE** R. & W. R. Bedford, 1934

DIAGNOSIS. Cups growing from an apex without central cavity, occupied by rods, plates and dissepiments. Adult stages with more or less definite radial septa, the pores of which are arranged in rows inclined upwards and outwards from inner to outer wall. Dissepiments and sometimes synapticulae present. Simple porous outer and inner walls, with the pores sometimes screened by a microporous sheath or pellis.

COMPOSITION OF THE FAMILY. *Protopharetra* Bornemann 1887, *Volvacyathus* Debrenne 1961, *Dendrocyathus* Okulitch & Roots 1947, ? *Shidertycyathus* Krasnopeeva 1959, *Metaldetes* Taylor 1910, *Cambrocyathus* Okulitch 1937, *Cambrocyathellus* Zhuravleva 1960, *Okulitchicyathus* Zhuravleva 1960, *Paranacyathus* R. & J. Bedford 1937, ? *Ardrossacyathus* R. & J. Bedford 1937, *Metafungia* R. & W. R. Bedford 1934.

Genus ***METALDETES*** Taylor, 1910

1910 *Metaldetes* Taylor : 151, pl. 15, figs. 86–88, t.-figs. 11, 37 and 38.
1934 *Metacyathus* R. & W. R. Bedford : 5.
?1957 *Bedfordcyathus* Vologdin : 182 and 209.

TYPE SPECIES. By monotypy *Metaldetes cylindricus* Taylor 1910, the holotype of which is in the University of Adelaide.

DIAGNOSIS. Solitary, or sometimes colonial cups; the central cavity and the inner wall slowly develop later. In the lower part of the cup, the irregularly arranged skeletal structures (bars, rods, plates and vesicular tissue) fill the whole inner space. Much later, the central cavity is defined by the formation of a regularly porous inner wall and the structures of the intervallum are arranged in radial plates; the tangential links (synapticulae and dissepiments) may continue into the adult stage.

Unfortunately, the type specimen of the genus has not been re-described yet and one has to rely on the original account and illustrations. According to Taylor (1910 : 151), the rugose character of the outer wall causes a transverse section to resemble a series of tridents. R. & W. R. Bedford (1934 : 5) considered the outer wall to be a double porous sheath, and my own observations agree with this (Debrenne 1964 : 219). Hill (1965 : 119) mentions that the longitudinal ribs between the rows of pores are connected together, some distance behind the outer edge, by transverse bars. The inner wall, which is absent in the lower part of the cup, was described by Taylor (1910 : 152) as being " strongly ridged on its septal side ". These ridges correspond to the beginnings of the taeniae, which are slightly thickened towards the inner wall. The number of pores per intersept is not certain (1, 2, or 3), nor their shape and size.

DISCUSSION. A complete revision of the type material is desirable, but although *Metaldetes* is incompletely known, it is possible to regard two subsequent genera, *Metacyathus* Bedford and *Bedfordcyathus* Vologdin, both found at the same locality and level, as synonyms. Okulitch (1955 : E 16), Zhuravleva (1960 : 283) and myself (Debrenne 1964 : 220) have previously considered *Metacyathus* a synonym of *Metaldetes*, but Vologdin (1957 : 43) and Hill (1965 : 118) thought it to be a separate genus. R. & W. R. Bedford established the genus to include those species in which the taeniae occur as straight radial septa in the inner two-thirds of the intervallum, but are separate from the outer wall, as in the type *M. taylori* R. & W. R. Bedford

Examination of the holotype of *M. taylori* shows that the structures of the intervallum are disturbed by the occurrence of exothecal lamellae, but that, at other levels, the plates continue from one wall to the other. The porosity of the outer wall depends on the presence or absence of the exotheca; the inner wall has one vertical row of pores per intertaenial space in the lower part of the cup, but two or more in the upper part, with probably a second wall.

Bedfordcyathus was established by Vologdin, after he had studied Bedford's figures, to group into a separate genus those species that have a strong development of vesicular tissue. The holotype of the type species (*M. irregularis* Bedford), now in the British Museum (Natural History), is described below. It shows that there is no appreciable difference from *Metacyathus*, in the structure of the intervallum (apart from the abundance of vesicular tissue), or in that of the walls. I think that vesicular tissue is too inconstant and variable a character to be sufficient grounds for establishing a new genus.

The genus *Metaldetes* is therefore defined as consisting of cups which grow from a base that does not have a distinct central cavity, where the skeletal elements have not attained a clear radial arrangement, and where tangential links (synapticulae and vesicular tissue) are numerous. Subsequently, the central cavity is differentiated by a more definite development of the inner wall, which is, at first, part of the intervallum (with one pore per intertaenial space), but then becomes a more distinct structure (with two pores per intertaenial space) and is, perhaps, protected on its central cavity side by a microporous sheath or vesicular membrane. At this same level, the intervallar elements generally form strong, compact, radial taeniae with high oval pores the diameter of which increases along upwardly curving lines from the inner to the outer wall; the largest pores being close to the outer wall. It is in this region that positional changes and external influences occur, the septa become less regular and sometimes revert to curved taeniea. The synapticular links may persist but generally disappear in the adult stage, whereas vesicular tissue is still abundant. The outer wall has a basic layer with irregular polygonal pores, overlapped by a second microporous sheath, which disappears when the cup is surrounded by exothecal lamellae. Fossils reach considerable size.

RELATIONSHIPS AND DIFFERENCES

Volvacyathus Debrenne 1961 has two distinct stages, the apex being quite different from the adult. The walls are still connected with the intervallar network, the septa are not clearly defined and their pores are wider than the intervening skeletal tissue. This genus is also close to *Protopharetra* Bornemann 1887.

Cambrocyathus Okulitch 1937 closely resembles *Metaldetes* in having abundant vesicular tissue, but the adult stage is reached more quickly. The central cavity is not free and is filled by thin skeletal rods and vesicular tissue, which persists as a pellis to the top of the cup. These structures are also found as an exotheca. The well-developed taeniae generally have a laminated structure and are perforated by pores, that are almost in horizontal lines. Scarce synapticulae or branching septa, but abundant vesicular tissue, which earlier authors have interpreted as true synapticulae. Reference material on loan from the Geological Survey of Canada and a topotype from the Yale Peabody Museum showed these features (Text-fig 14).

Septa of *Cambrocyathus*-type (see Debrenne 1964 : 88) are the final stage in the process of radial partition. This starts with *Protopharetra*, leads through *Volvacyathus* (see Debrenne 1964, fig. 51) and the first *Metaldetes* (*proteus* and *dissutus*), with their broken septa, to the complete septa of *Metaldetes irregularis* and finally, to the regular septa of *Cambrocyathus*.

COMPOSITION OF THE GENUS. *M. cylindricus* Taylor 1910, *M. columbianus* (Okulitch 1943), *M. dissepimentalis* (Taylor 1910), *M. dissutus* Debrenne 1964, *M. irregularis* (R. & W. R. Bedford 1934), *M. ramulosus* R. & J. Bedford 1937, *M. solidus*

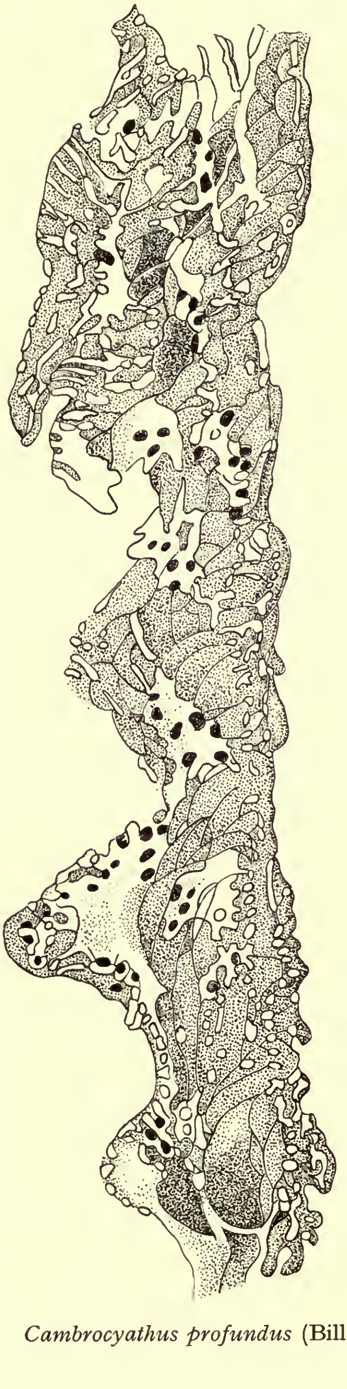

FIG. 14. *Cambrocyathus profundus* (Billings) ×4

(Okulitch 1957), *M. spiralis* R. & W. R. Bedford 1936, *M. superbus* R. & W. R. Bedford 1936, *M. taylori* (R. & W. R. Bedford 1934), *M. proteus* (Bornemann 1887).

Metaldetes dissepimentalis (Taylor)

(Pl. 16, figs. 1–3)

1910 *Archaeocyathus dissepimentalis* Taylor : 128, pl. 10, fig. 53.
1934 *Metaldetes conicus* R. & W. R. Bedford : 5, figs 26, 28 and 31.
1936 *Metaldetes conicus* R. & W. R. Bedford : 18, pl. 18, fig. 77.

HOLOTYPE. Possibly at Adelaide University.

MATERIAL. B.M. (N.H.) S 4176–4182.

DESCRIPTION. Large conical cups. In the first stages, the central cavity is not formed and the entire cup is occupied by un-orientated taeniae, which are joined by numerous dissepiments that are arranged as horizontal vesicles. Much later, the cavity develops, the dissepiments become less abundant and the taeniae form regular radial plates. The general aspect recalls that of *Cambrocyathus profundus* Billings.

The outer wall is twofold: a basal wall covered externally by a very thin microporous sheath. The inner wall is also double; the main wall having two rows of large irregular pores per intersept, with the diameter of the pores being much greater than the width of the skeletal tissue between them; with a microporous sheath, similar to that of the outer wall, occurring on the central cavity side. The microporous sheaths are not well known for they are often eroded and no good tangential sections have been seen. Consequently, the arrangement, size and shape of the micropores is not certain, they appear to be similar to those of the secondary wall in *Metafungia*.

DIMENSIONS

	S 4176	S 4178	S 4179 S 4180 low.	S 4180 up. S 4181	S 4182	*dissepimentalis* Taylor
	(mm.)	(mm.)	(mm.)	(mm.)	(mm.)	(mm.)
Cup:						
Height (*pars*)	60	..	..	15	40	
Diameter	24	13	13	21	45	22
Intervallum	6	4	..	6	7·5	6
Interseptum	0·4–0·7	0·5	0·7	0·5	1·35	7
Intervallum coefficient	0·5	0·8	..	0·6	0·25	0·6
Outer wall:						
No. of rows of pores per interseptum	1–3	1–3	2	2	1–3	2
Diameter	0·17	0·33	0·2	0·20	0·25–0·40	0·30
Skeletal partitions	0·30	0·20	0·15	0·15	0·15–0·20	0·20
Micropores: diameter	0·03	..	0·06	0·06	..	..
skeletal partitions	..	..	0·06	0·06	..	..
Thickness	0·20	0·20	..	..	..	..

Dimensions—*continued*

	S 4176 (mm.)	S 4178 (mm.)	S 4179 S 4180 low. (mm.)	S 4180 up. S 4181 (mm.)	S 4182 (mm.)	*dissepimentalis* Taylor (mm.)
Inner wall:						
No. of pore rows per interseptum	2	2	..	1–3	1–2	1–2
Diameter	0·67	0·47	..	0·33	0·33	0·30
Skeletal partitions	0·16	0·16	..	0·10	0·10	0·10
Micropores: diameter	..	..	..	0·03	0·03	0·03
skeletal partitions	..	..	..	0·03	0·03	0·03
Thickness	..	..	..	..	..	..
Septa:						
Diameter	0·40	..	..	..	0·40	0·20
Skeletal partitions	..	..	..	..	0·40–0·60	..
Thickness	0·13	..	..	0·13	0·20	0·20

Discussion. The description and figures given by Taylor for *Archaeocyathus dissepimentalis* correspond with measurements taken from the photographs of *Metaldetes conicus* Bedford. The two species are, therefore, considered to be synonymous and *dissepimentalis*, the older, is the name conserved.

Metaldetes irregularis (R. & W. R. Bedford)

(Pl. 16, fig. 4)

1934 *Metacyathus irregularis* R. & W. R. Bedford : 6, pl. 5, fig. 29.
1957 *Bedfordcyathus irregularis* (Bedford) Vologdin : 43.
1964 *Metacyathus-Bedfordcyathus irregularis* (R. & W. R. Bedford); Debrenne : 220 and 231.
1965 *Bedfordcyathus irregularis* (R. & W. R. Bedford); Hill : 118, fig. 22.9.

It has not been possible to locate the original description by Vologdin of his genus *Bedfordcyathus*. Both Debrenne (1964) and Vologdin (1957, 1962) give the year 1955 for this genus, but, unfortunately, there is no mention of *Bedfordcyathus* in the paper cited under that year, in either bibliography (*Dokl. Akad. Nauk SSSR*, **103**, 1). In subsequent papers, Vologdin gives the year as 1956, but the only paper available for that year merely includes the genus in a list showing the classification of the Archaeocyatha. This paper appeared in a slightly more elaborate form during 1957, in two journals: *Acta paleont sinica*, **5**: 173–222 and *Annls. Cent. Etud. Docum paleont.*, **23** : 33–80 and it is the latter, which is taken as the basis of the date given in this paper and that of Hill (1965). However, it would appear that the paper referred to, is included in the yet unpublished Vol. 3 of " *El sistema Cambrico . . .* ", Int. Geol. Congr. Mexico, 1955, quoted in some references as 1961.

Holotype. B.M. (N.H.) S 4189, by monotypy.

Other Material. Paratypes B.M. (N.H.) S 4188, S 4190.

Description. Conical cup, with large irregularly-waved intervallum. Double outer wall; first, a thick basal one, pierced by funnel-shaped pores that widen towards the exterior; this is covered externally by a very thin microporous sheath. The inner wall is not well known, but from a small poorly preserved surface, appears to be covered by an irregular, microporous, thin wall, which screens the simple pores of the intervallum.

The taeniae in the upper part, are straight, radial and completely cross the intervallum. In longitudinal section, the pores appear circular and alternate in regular lines, curving shallowly towards the exterior from the inner to the outer wall. The skeletal tissue and the pores, occupy equal proportions of the total surface area. Considerable development of vesicular tissue, formed of imbricate, horizontally elongated vesicles, that cross several loculi, but do not penetrate into the central cavity.

DIMENSIONS

	(mm.)
Cup:	
Height (*pars*)	92
Diameter	about 35
Intervallum	10
Intervallum coefficient	0·6
Interseptum	1·35
Outer wall:	
No. of rows of pores per interseptum	2
Diameter of pores	0·27
Partitions	0·20–0·40
Micropores	0·10
Inner wall:	
Diameter of pores	0·35–0·67
Partitions	0·13
Micropores	4 to each main pore
Diameter of micropores	0·05
Thickness	0·06
Taeniae:	
Diameter of pores	0·33–0·54
Partitions	0·27–0·33

DISCUSSION. The strong development of vesicular tissue and the absence of exothecal lamellae, are the main differences between this species and others in the genus.

Metaldetes taylori (R. & W. R. Bedford)

(Pl. 13, figs. 1–3)

1934 *Metacyathus taylori* R. & W. R. Bedford : 5, pl. 5, fig. 10.
1936 *Metacyathus taylori* R. & W. R. Bedford; R. & W. R. Bedford : 18, pl. 18, fig. 80.
1964 *Metaldetes taylori* (R. & W. R. Bedford) Debrenne : 220.
1965 *Metacyathus taylori* R. & W. R. Bedford; Hill : 118, pl. 9, figs. 2a–d.

HOLOTYPE. By monotypy, B.M. (N.H.) S 4185–4187 (three pieces of the same specimen).

DESCRIPTION. Although the three pieces are said to come from the same cup, it is no longer possible to prove this with any certainty, for having been subjected to various palaeontological techniques (cutting, etching etc.), they do not fit together.

Nevertheless, there is little chance of the lower part belonging to another specimen. This is pointed out because the lower part has some structures obviously different from the other two pieces and these are important for generic determination.

The lower part is conical; radial, slightly porous taeniae are connected by synapticulae, which develop between the pores. The inner wall has a single row of pores per interseptum. The outer wall is well defined and separates the intervallum from the exothecal lamellae. Dissepiments present.

In the middle and upper parts of the cup, the inner wall has two rows of pores per interseptum; the outer wall is not yet separate from the exothecal structures, which disturb the outer part of the intervallum and give the septa the form of curved taeniae. No synapticulae, but dissepiments persist. The pseudo-septa are mainly radial at the inner and middle parts of the intervallum, but are interrupted towards the outer wall and disappear near the exothecal lamellae.

DIMENSIONS

	S 4185 Apex (mm.)	S 4186 (mm.)		S 4187 (mm.)
Cup:				
Height (*pars*)	35	55		40
Diameter	16	35	upper	35
		24	lower	
Intervallum	4	11	upper	10
		7	lower	
Intervallum coefficient	0·72	0·8	upper	1
		0·7	lower	
Interseptum	0·33	1		1
Outer wall:				
Thickness	0·06	disappeared		disappeared
Inner wall:				
No. of pore rows per interseptum	1	2		2
Diameter	..	0·33		0·33
Skeletal partitions	..	0·20		0·20
Thickness	..	?		?
Taeniae	..	0·40–0·60		0·60
Diameter of pores	..	0·40		0·40
Thickness	..	0·27		0·25

DISCUSSION. *Metaldetes taylori* (R. & W. R. Bedford) differs from *M. irregularis* (R. & W. R. Bedford) by its narrow central cavity, weak development of vesicular tissue and the abundance of exothecal lamellae. It is little different from *M. dissepimentalis* (Taylor), which has straighter septa, a well-defined, double-porous outer wall, but is without any exothecal lamellae.

Genus ***METAFUNGIA*** R. & W. R. Bedford, 1934

1934 *Metafungia* R. & W. R. Bedford : 5.
1964 *Metafungia* R. & W. R. Bedford; Debrenne : 219
1965 *Metafungia* R. & W. R. Bedford; Hill : 119.

TYPE SPECIES. *Metafungia reticulata* R. & W. R. Bedford, by monotypy.

Diagnosis. Cup with central cavity that becomes free of skeletal tissue late in its development. The walls are double-porous. The intervallum is crossed by straight taeniae, which have their pores arranged in lines curving upwards and outwards; numerous synapticulae join the taeniae. The vesicular tissue is present at the base and in contact with tersioid outgrowths.

Composition of the Genus. *Metafungia reticulata* R. & W. R. Bedford.

Metafungia reticulata R. & W. R. Bedford

(Pl. 18, figs. 1–3)

1934 *Metafungia reticulata* R. & W. R. Bedford : 5, figs. 23 a–e.
1965 *Metafungia reticulata* R. & W. R. Bedford; Hill : 119, pl. 10, fig. 2 and text-fig. 22, 12 a–d.

Holotype. B.M. (N.H.) S 4184. Other Material S 4183.

Description. Large conical cup, the apex is surrounded by exothecal tersioid outgrowths and the central cavity is filled with endothecal tissue. The intervallum is crossed by straight, radial taeniae, which are perforated by pores, aligned upwards and outwards, in oblique rows. The diameter of these pores increases from the inner to the outer wall, giving an irregular appearance. The numerous synapticulae connect at the skeletal junctions of the taeniae. The vesicular tissue is only developed in the exo- and endothecal regions. The intervallar mesh, with some development of skeletal tissue and vertical closing of the apertures, corresponds to an outer wall. A regular micro-porous thin wall covers this externally. The inner wall may also be interpreted as a double wall. The inner part of each taenia has pores no larger than 0·7 mm; these taeniae are joined by small plates, resembling widened synapticulae, to form a small tube. On the central cavity side, a thin sheath is developed, with two pores to each tube, and has a more or less regular, hexagonal appearance.

Dimensions

	S 4183 Base (mm.)	(mm.)	S 4184 Top (mm.)
Cup:			
Height	..	35	..
Diameter	12	..	21
Intervallum	2·5	..	5
Intervallum coefficient	0·3	..	0·4
Interseptum	0·8	..	1·01
Synapticulae: radial distance	..	..	0·61
vertical distance	..	..	0·61
Outer wall:			
Diameter of main pores	..	0·70	..
Partitions	..	0·27	..
Thickness	..	0·2	..
Micropores: diameter	..	0·07	..
partitions	..	0·06	..

DIMENSIONS—*continued*

	S 4183 Base (mm.)	(mm.)	S 4184 Top (mm.)
Inner wall:			
Diameter of tubes	..	0·7–0·7	..
Partitions	..	0·27	..
Length of tubes	..	0·70	..
Inner pores: diameter	..	0·20	..
partitions	..	0·13	..
Septa:			
Thickness	..	0·13	..
Diameter of inner pores	..	0·25	..
Diameter of outer pores	..	0·40	..
Synapticulae:			
Thickness	..	0·13	..

DISCUSSION. *Metafungia reticulata* has an intervallar structure similar to that of *Flindersicyathus graphicus* (R. & W. R. Bedford). However, its size is much greater and the connecting synapticulae do not occur at every skeletal junction, but the essential difference is in the structure of the walls.

Family **METACOSCINIDAE** R. & W. R. Bedford

DIAGNOSIS. Two-walled porous cups. Taeniae and sparse convex tabulae.

COMPOSITION OF THE FAMILY. *Metacoscinus* R. & W. R. Bedford 1934, *Pycnoidocoscinus* R. & W. R. Bedford 1936, *Paracoscinus* R. & W. R. Bedford 1936, *Claruscyathus* Vologdin 1932, *Gabrielsocyathus* Debrenne 1964.

Genus ***METACOSCINUS*** R. & W. R. Bedford

1934 *Metacoscinus* R. & W. R. Bedford : 6, pl. 5, fig. 27.
1965 *Metacoscinus* R. & W. R. Bedford; Hill : 133, pl. 12, fig. 1, text-fig. 5 a–d.

TYPE SPECIES. *Metacoscinus reteseptatus* R. & W. R. Bedford, by monotypy.

DESCRIPTION. Conical cups, slightly waved externally. Oblique and vertical rods form the skeletal tissue of taeniae crossing the intervallum. These rods have considerable openings between them, which are much taller than wide and are roughly polygonal in shape. The outer pores are the largest. Less frequent horizontal structures regarded as tabulae, are perforated by small circular pores, that are separated by " linteaux " of varying size, and bear little irregular tubercles on each side.

Outer wall has funnel-shaped pores, circular on the intervallum side, larger and more irregular on their open outer side. Thin inner wall with two rows of large polygonal pores per intersept, separated by a thin skeletal mesh. R. & W. R. Bedford figured a specimen (1936 : fig. 83), which had several tubercles on its central cavity side.

Composition of the Genus. *Metacoscinus reteseptatus* R. & W. R. Bedford 1934, ? *Metacoscinus insigne* R. & W. R. Bedford 1936.

Discussion. *Metacoscinus insigne* is retained in this genus with some misgiving, until the type material can be revised. It has no visible tabulae and a thick outer wall with labyrinthoid pores. Nothing is known about the structure of these pores, whether their distorted shape is due to the fusion of several tubercles, as seen in the tabulae of *M. reteseptatus*, or results from lateral connection between neighbouring pore-tubes.

I have had the opportunity to examine the type material of *Metacoscinus gabrielsensis* (Okulitch 1955), *M. deasensis* (Okulitch 1955) and *M. poolensis* (Kawase & Okulitch 1957) loaned by the Geological Survey of Canada and have already suggested (Debrenne 1964 : 248), that these species should be regarded as a separate genus, *Gabrielsocyathus* Debrenne 1964, with *G. gabrielsensis* (Okulitch) as type species. This differs from *Metacoscinus* in having simply-porous, regularly-spaced tabulae; branching, or waved porous taeniae; a double, porous, outer wall with exotheca; endothecal lamellae partially filling the central cavity and extremely abundant vesicular tissue.

The species *poolensis* (Kawase & Okulitch) is included in *Gabrielsocyathus* with some reservations. The septa appear to undulate and bifurcate and have fewer pores than the other two species; the plates thicken at the junction with the septa; no exotheca occurs and the vesicular tissue is less abundant. The poor preservation of the specimen prevents confirmation of the presence of fine, irregular pores in all the skeletal plates.

Zhuravleva (1960 : 311) remarks that *Paracoscinus* and *Metacoscinus* are very close to each other and goes on to suggest that they might represent one genus, but since she had no material, it was difficult to make a definite decision. I have not seen the type of *Paracoscinus*, but from the figures and descriptions of R. & W. R. Bedford (1936 : 18, pl. 20, figs. 85–86), I consider that it differs from *Metacoscinus* in its wall structure (microporous and not a large open mesh); the abundant and regular plates, which have polygonal pores and are without tubercles; the thin outer wall and the inner wall with a single row of pores per interseptum.

Metacoscinus reteseptatus R. & W. R. Bedford

(Pl. 17, figs. 1–4)

1910 *Archaeocyathus retesepta* Taylor : 120, pl. 7, figs. 39–40.
1934 *Metacoscinus reteseptatus* R. & W. R. Bedford : 6, pl. 5, fig. 27.
1936 *Metacoscinus reteseptatum* R. & W. R. Bedford; R. & W. R. Bedford; 18, pl. 19, fig. 83.
1965 *Metacoscinus reteseptatus* R. & W. R. Bedford; Hill : 132–3, pl. 12, fig. 1, text-fig. 24, 5 a–d.

Material. Syntypes B.M. (N.H.) S 4191–4195. Other material S 4762, S 4772, S 4743, S 7633.

Description. Conical cups with transverse annular bulges. Outer wall has two vertical rows of funnel-shaped pores per intersept, the larger aperture on the outside, with an irregular rim. Inner wall, also, has two vertical rows of pores, but these are polygonal and separated by very thin skeletal rods, without tubercles. Regular, radial pseudosepta, perforated by numerous hexagonal pores that are elongated upwards, or upwards and outwards in the annular bulges. Little vesicular tissue except in the lower part, where the pseudosepta are not so well developed and skeletal elements fill both the central cavity and the intervallum. Sparse tabulae, which have tubercles occurring between their two rows of quincunxial pores per intersept. The regular pattern of the pores is disturbed by the coalescence of neighbouring pores, or by anastomosed tubercles, giving these horizontal plates a vermiculate aspect, when seen from above.

DIMENSIONS

	S 4191 (mm.)	S 4192 & S 4193 low (mm.)	S 4193 upper (mm.)	S 4195 (mm.)	S 4762 (mm.)
Cup:					
Height (pars)	21	base	..	25	20
Diameter	12	7	10	25–30	15
Intervallum	2	..	2	6	2·45
Central cavity	8	full	4	11	unknown
Interseptum	0·35	0·22	0·26	0·75	0·22
Intertabulum	1·7–3·4	..	..	..	..
Outer wall:					
No. of pore rows per interseptum	2–3	..	2	2	2
Diameter	0·15	..	..	0·18	0·15
Vertical partitions	0·06–0·10	..	..	0·15	0·06–0·10
Horizontal partitions	0·06–0·10	..	..	0·15	0·10
Thickness	0·30	0·26	..	0·18	unknown
Inner wall:					
No. of pore rows interseptum	2	..	2	2–3	1–2
Diameter	0·07	..	0·07	0·18–0·37	0·22–0·30
Vertical partitions	0·07	..	0·07	0·07	0·07
Horizontal partitions	0·07	..	..	0·07	0·15
Thickness	0·20	..	0·11	0·11	unknown
Septa:					
No. of pore rows	..	..	6	..	unknown
Diameter	0·15–0·37	..	0·22–0·40	0·56–1·51 0·26–0·52	0·26
Vertical partitions	0·07	..	0·07	0·18	0·13
Horizontal partitions	0·11	..	..	0·18	..
Thickness	..	..	0·07	0·11	0·07
Tabulae					
No. of pore rows	2	..	..	..	..
Diameter	0·11	..	..	..	..
Vertical partitions	0·11	..	..	..	..
Horizontal partitions	0·11	..	..	..	..
Thickness	0·15	..	..	..	..

DIMENSIONS—*continued*

	S 4772 (mm.)	S 4743 (mm.)	S 4743 lower (mm.)	S 4194 lower (mm.)	S 4194 upper (mm.)	S 7633 (mm.)	*retesepta* Taylor (mm.)
Cup:							
Height (pars)	unknown	12	..	30	..	..	90
Diameter	16	10	7	9	16	15	25
Intervallum	3·5	2	1·35	1·45	4·8	4	..
Central cavity	..	..	4·3 clear	skel. el.	..	..	..
Interseptum	0·5	0·22	0·33	0·41	0·37	0·34	0·45
Intertabulum	..	..	..	..	..	..	..
Outer wall:							
No. of pore rows per interseptum	2	2–3	unseen	2	2	..	2
Diameter	..	0·13	..	0·26–0·15	0·26–0·26	..	0·20
Vertical partitions	..	0·07	..	0·05	0·26–0·18	..	0·11
Horizontal partitions	..	..	..	..	0·11	..	..
Thickness	..	0·11	..	..	0·18	0·11	..
Inner wall:							
No. of pore rows interseptum	2	unseen	2	unseen	unseen	2–3	2–3
Diameter	..	..	unseen	..	0·18	0·15	0·15
Vertical partitions	..	..	..	..	0·07	0·11	0·10
Horizontal partitions	..	..	..	..	..	..	..
Thickness	..	..	0·07	..	0·11	0·11	0·10
Septa:							
No. of pore rows	7	..	7	5	7	..	..
Diameter	0·45	0·13–0·22	0·13	0·49	0·34–1·7	0·26	0·35
Vertical partitions	0·11	0·07	0·07	0·07	0·15	0·11	0·15
Horizontal partitions	..	..	..	0·15	0·15	..	..
Thickness	0·15	0·11	0·07	0·11	0·11	0·11	0·15
Tabulae:							
No. of pore rows	..	..	..	..	..	..	..
Diameter	..	..	..	..	0·11	..	..
Vertical partitions	..	..	..	..	0·10	..	..
Horizontal partitions	..	..	..	..	not visible	..	..
Thickness	..	..	..	..	0·15	..	..

DISCUSSION. R. & W. R. Bedford (1934 : 6) compared this species with *Archaeocyathus retesepta* Taylor, noting the likeness between the taeniae, but no horizontal structures were known in *A. retesepta*. Nevertheless, from Taylor's figures (Pl. 7, figs. 39 and 40), one can perhaps consider that the structures normal to those in the general direction are the beginnings of tabulae. Amongst all the specimens in the Bedford collection at the British Museum (Nat. Hist.), only S 4195 and S 4194 show these rare horizontal structures. The dimensions of the two species are of the same order and they are probably synonymous. Before joining them as a single species we need more material, in order to know the frequency and significance of these horizontal structures and to decide whether they have any systematic value, or are true tabulae, or are accidental features.

? Family **METACOSCINIDAE** R. & W. R. Bedford, 1936

Genus ***PYCNOIDOCOSCINUS*** R. & W. R. Bedford, 1936

1936 *Pycnoidocoscinus* R. & W. R. Bedford : 19, pl. 20, fig. 87.

TYPE SPECIES. *Pycnoidocoscinus pycnoideum* R. & W. R. Bedford, by original designation.

DIAGNOSIS. Cups with annular bulges on the outer wall, with the inner wall remaining cylindrical. Radial septa and arched tabulae. The outer wall is a porous mesh; the inner wall with both horizontal and vertical rows of rectangular pores.

DISCUSSION. As the early stages are not known, it is difficult to classify this genus in either the Irregularia—indicated by the irregular outer wall and septa with numerous pores, or amongst the Regularia—as suggested from the type of inner wall with its rectangular apertures, the tabulae with the axis of curvature inside the intervallum, or the pore pattern of *Retecoscinus*-type. Only having examined a single broken fragment, it is not possible for me to offer any solution and the genus *Pycnoidocoscinus* is retained in the Metacoscinidae, but with some reservations.

COMPOSITION OF THE GENUS. *Pycnoidocoscinus pycnoideum* R. & W. R. Bedford.

Pycnoidocoscinus pycnoideum R. & W. R. Bedford

(Pl. 18, figs. 4–8)

1936 *Pycnoidocoscinus pycnoideum* R. & W. R. Bedford : 19, pl. 20, fig. 87.

MATERIAL. B.M. (N.H.) S 4832. A syntype P 990 is in the South Australian Museum, Adelaide.

DESCRIPTION. Only one weathered and poorly preserved specimen has been examined. The intervallum is crossed by radial septa and arched tabulae. The septa are thickened near the inner wall and sometimes near the outer wall, but are very thin in the middle. Septal pores are not visible. Pores on a small, tangential surface of a tabula resemble those of *Retecoscinus* Zhuravleva (1960), with two alternating rows of oval to rectangular pores.

Outer wall eroded away; R. & W. R. Bedford have described it as " a layer of fine pores supported by an irregular mesh ". Inner wall has two rows of pores per interseptum and two rows of pores per intertabulum.

The vertical partition between the two interseptal pores, is the beginning of a new septum, which only develops in the inner third of the intervallum. Sometimes opposite this crude septa, another arises from the outer wall to meet it.

DIMENSIONS

	(mm.)
Cup:	
Height (*pars*)	30
Diameter	22
Interseptum (at the inner wall side)	0·33
Intertabulum	1·22

DIMENSIONS—*continued*

	(mm.)
Outer wall:	weathered away
Inner wall:	
Diameter of pores	0·33
Vertical partitions	0·1
Horizontal partitions	0·06
Septa	
Diameter of pores	0·06
Vertical partitions	0·2
Thickness: middle	0·06
near inner wall	0·2
Tabulae:	
No. of pores per loculus	2×22
Diameter of pores	0·27–0·1
Partitions	0·1–0·13
Thickness	0·1

DISCUSSION. The rows of rectangular pores of the inner wall and the presence of " rods " in the middle of the interseptum (interpreted here as the beginnings of new septa) are good reasons for including S 4832 in *P. pycnoideum*. Unfortunately, poor preservation and the lack of an apex prevents any clarification of the systematic position of *Pycnoidocoscinus*.

III. STRATIGRAPHICAL CONCLUSIONS

The excellent silicified fossils found in the Australian Cambrian, as well as being extremely useful for anatomical studies of the Archaeocyatha, are also of considerable stratigraphical interest.

We have little information on the precise horizon in the Ajax Limestone, from which the Bedfords collected their fossils. According to Daily (1956 : 129), " . . . Most, if not all, of the species described from the Ajax Mine area by Taylor and the Bedfords, are believed to have come from beds containing this assemblage [i.e. faunal assemblage No. 1], for it is significant that no fossils characteristic of faunal assemblage No. 2 have been reported by them. Such fossils would almost certainly have been noticed if they were present . . .". However, Walter (1967) comments (p. 145) that the rich Ajax fauna described by the Bedfords & Taylor, cannot be placed in Daily's scheme of faunal units. This is because, in an area of complex structure, it was not collected in sequence and the additional evidence of the fauna associated with the archaeocyathids is not available. As a result it is of very limited stratigraphical use.

The out-dated studies of Taylor and the too brief publications of the Bedfords, have not allowed specialists in other countries to make precise comparisons and possible correlations, between their material and that of Australia. An attempt was made on the limited material available in the Ting collection (F. & M. Debrenne 1960). It was concluded, from the majority of genera appearing at Beltana, that the fauna belonged to the Aldanian and Lower Lenian stages. Since then, I have become acquainted with Russian work that amends the stratigraphical correlation between the Southern Siberia geosyncline and the Siberian platform, and gives detailed lists of revised Archaeocyatha faunas from level to level.

These data, together with the present study, confirm that the Ajax Limestone is situated in the lower half of the Lower Cambrian; to be precise, the fauna is similar to that of the Kameshki horizon and also has a certain affinity with those forms found in the succeeding Sanashtygkol horizon. This opinion is based on the presence, in the Ajax fauna, of forms having advanced evolutionary stages of outer and inner walls, or intervallar structures, together with other simple forms known from the Bazaikha horizon, such as *Monocyathus*, *Alphacyathus*, *Ajacicyathus*, *Robustocyathus* and *Erismacoscinus*.

As examples of the advanced forms, one can show the presence of genera with:

1. Outer walls with simple tumuli (*Tumuliolynthus*, *Ethmocoscinus*), or multiperforate (*Alataucyathus*).

   According to Rozanov (1963 : 8) genera with tumuli mainly arise in the Kameshki horizon.

2. Double porous outer wall (*Tomocyathus*, *Polycoscinus*).

   This feature appears at the end of the Bazaikha horizon and genera that possess it increase in numbers through the Kameshki and Sanashtygkol horizons.

3. Inner wall with complex annular rings.

   This is seen in *Cyathocricus annulispinosus* (Vologdin) found in the Kameshki horizon of Eastern Sajan, and the Australian species *annulatus* (Bedford) regarded as belonging to *Salairocyathus*, which occurs in the Sanashtygkol horizon.

4. Inner wall with branching pore-tubes (*Zonacyathus*).

   Three Russian species probably belong to this genus; *poletaevae*, *vermiculatum* and *flexum*. They and the corresponding colonial genus *Sajanocyathus* are of Sanashtygkol age.

5. Radial septa with few, or no pores (*Cyathocricus*, *Ethmocyathus*, *Zonacyathus*, *Robustocyathus subacutus* and *Archaeocyathellus* (*Stapicyathus*) *stapipora*).

   Zhuravleva (1960 : 147) and Rozanov & Missarzhevsky (1966 : 71) consider that the decrease or loss of septal porosity is an evolutionary character of the Regularia. The pores of the plates are often different to the septal pores in Australian *Coscinocyathus*, whereas in specimens found at lower levels in the Cambrian (e.g. Soussian horizon in Morrocco) they are very similar. The first appearance of any difference between the two occurs in the Sardinian limestones, contemporaneous with the Botoma Stage of Southern Siberia.

Lower Cambrian

These correlations are taken from Table II of Walter (1967), who used information given in a personal communication (Sept. 1966) to M. F. Glaessner by A. Yu. Rozanov.

Siberian platform		Geosyncline of southern siberia	
	Lower subdivision		
TOMMOT STAGE	Sunnagin	ALDAN STAGE	Kundatsk horizon
	Kenyada		Bazaikha horizon
	Atdaban		Kameshki horizon
	Tarynsk		
	Sinsko-Kutorgina	BOTOMA STAGE	Sanashtygkol horizon

Upper subdivision		
Ketema	LENA STAGE	Solontsov horizon
Elanka		Obruchev horizon

Similar studies of evolutionary stages, have not been made for the Irregularia, but it is possible to make the following points.

1. The first Irregularia have scattered skeletal elements, rods, or plates, as in *Dictyocyathus*, or *Protopharetra* and are of Soussian age. They then follow two particular paths.
    - a. The plates of *Protopharetra* gave rise to the crude pseudo-septa of *Volvacyathus*-type, where the pores occupy a greater surface area than the skeletal tissue; then into the poorly developed pseudosepta shown in the first *Metaldetes* of Sardinia; followed by the definite radial septa of the true *Metaldetes* of Australia and ending with the *Cambrocyathus*-type, which occurs in the upper half of the Lower Cambrian.
    - b. The rods of *Dictyocyathus*, on the other hand, form the regular scaffolding of *Flindersicyathus* and *Pycnoidocyathus* types, which are comparable to the intervallar structure of Tabellaecyathidae Fonin, characteristic of the Sanashtygkol horizon.
2. Amongst the Ajax fossils one finds *Syringocnema*, a genus characterized by prismatic loculi in the intervallum. In the USSR the species referred to this genus are limited to the Sanashtygkol horizon.
3. The walls of the Irregularia are not so diverse as those of the Regularia. In the older forms of *Dictyocyathus* and *Protopharetra* they are not independent of the intervaller structural elements. This is attained in the genus *Flindersicyathus*, with its simply porous outer wall and inner wall having pore-tubes, the lower parts of which are modified and stretched. The double porous inner wall is seen in the genera *Metaldetes*, *Metafungia* and *Metacoscinus*. Such structures indicate the development of more advanced features, e.g. lamellae and tabulae, that are known in the Sanashtygkol horizon (Fonin 1963).

All these considerations show that there are clear affinities between the Ajax faunas and those of the Kameshki and Sanashtygkol horizons. The absence of forms with clathrate outer walls, or inner walls of true *Ethmophyllum*-type, shows that the Sanashtygkol fauna was not well established in Australia at the time of the Ajax limestone. The fauna is, therefore, probably of Upper Kameshki and Lower Sanashtygkol age, that is to say the middle part of the lower division of the Lower Cambrian.

Since this conclusion was first written Walter (1967), in his study on the usefulness of Archaeocyatha for zoning and correlation in the Lower Cambrian of the Adelaide Geosyncline, has correlated the various faunas in the Hawker Group of South Australia with those of Siberia. Using genera as the basis of such correlation, he has assigned a Sanashtygkol age to the Oraparinna Shale; the latter occurs above the

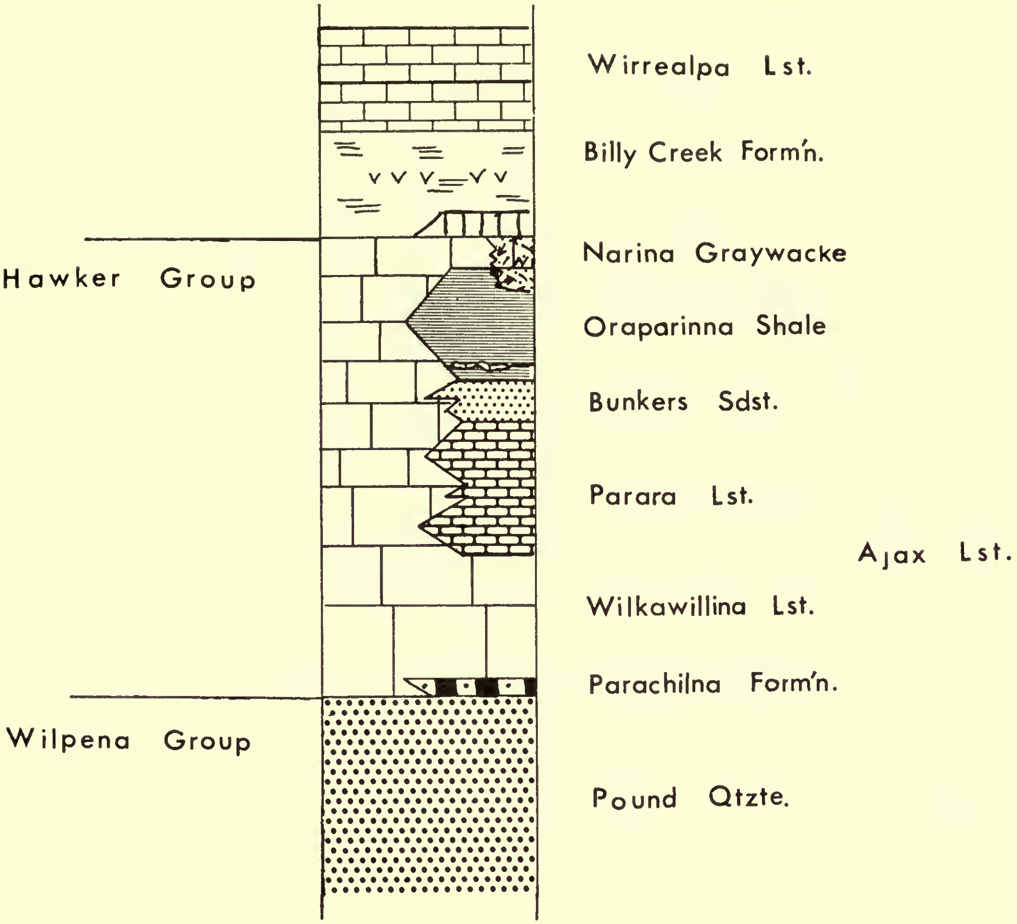
Wirrealpa Lst.
Billy Creek Form'n.
Narina Graywacke
Hawker Group
Oraparinna Shale
Bunkers Sdst.
Parara Lst.
Ajax Lst.
Wilkawillina Lst.
Parachilna Form'n.
Wilpena Group
Pound Qtzte.

FIG. 15. Lower Cambrian Sediments, Flinders Ranges; S. Australia. After Dalgarno (1964) & Walter (1967).

Wilkawillina Limestone of which, in the Mt. Scott Range area, the Ajax Limestone is said to be the equivalent (Dalgarno 1964 : 136). Commenting on the Ajax Limestone Walter (p. 146) suggests that the presence of *Syringocnema, Flindersicyathus* and *Pycnoidocyathus* indicate correlation with the upper part of the Hawker Group in the Wilkawillina Gorge section and concludes that, in the Ajax Mine area, the Ajax Limestone may be another bioherm. This evidence would appear to support my conclusions as to the age of the fauna of the Ajax Limestone.

IV. SUMMARY

The material now in the British Museum (Natural History), collected and originally described by R. & W. R. Bedford, has been revised according to current classification.

It is considered necessary to create a separate family within the Ajacicyathacea for the genus *Ethmocyathus*, which is characterized by a secondary wall of annular plates on the central cavity side of the inner wall. A new genus, *Cyathocricus*, is introduced for *Bronchocyathus* Bedford, which did not conform to the rules of zoological nomenclature, and includes those forms belonging to the Bronchocyathidae that have a more complex inner wall than *Cyclocyathus*. Two species are assigned to the new genus.

A new subgenus *Loculicyathus* (*Loculicyathellus*) is distinguished from *Loculicyathus* (*Loculicyathus*) by the longitudinal corrugations occurring between the septa on the outer wall. Two new subgenera are introduced for the smooth inner wall forms of *Tomocyathus: T.* (*Erugatocyathus*) and *Alataucyathus* : *A.* (*Anaptyctocyathus*). A new species of the latter is erected, *A.* (*A.*) *flabellus*, which is distinguished from *A.* (*A.*) *cribripora* by its bowl-shaped cup, dimensions and arrangement of wall pores.

In the broader classification, the family Acanthinocyathidae is distinguished from the Dokidocyathidae, and the family Bronchocyathidae is re-introduced to take the new genus *Cyathocricus*. The genus *Flindersicyathus* is included in the re-introduced family Flindersicyathidae, as there are many characters of this genus which distinguish it from *Archaeocyathus*. *Pycnoidocyathus* and *Flindersicyathus* are treated as subgenera until the Ajax Mine material in both Princeton and Adelaide is re-studied.

Owing to both the poor preservation and limited number of some specimens, it has been impossible to see sufficient structural details for exact determination and the true position of several genera remains uncertain. However, the good condition of other material has enabled a thorough study of the internal skeleton to be made, with the result that new types of structure have been discovered, e.g. the annular form of the inner wall in *Salairocyathus* (*S.*) *annulatus*.

From the stratigraphical evidence, it is concluded that the fauna is of middle Lower Cambrian age, i.e. upper Kameshki—lower Sanashtygkol horizons, and this has been borne out by subsequent work.

V. ACKNOWLEDGMENTS

I wish to thank Dr. E. I. White and Dr. H. W. Ball for the opportunity of studying the Bedford collection in the Department of Palaeontology. I would also like to thank Dr. Ball and Mr. S. Ware, for the generous help and information given to me whilst examining this collection. I am also extremely grateful to Professor M. F. Glaessner and his colleagues of the University of Adelaide and at the Geological Survey of South Australia, for allowing me to reproduce maps and stratigraphical information in text-figs. 13, 14 and 15. In addition, thanks are also due to my husband M. M. Debrenne and Mr. P. Green of the Photographic Studio at the B.M. (N.H.) for the photographs. Finally, I wish to thank Dr. Dorothy Hill, of the University of Queensland, for her encouragement and advice, and for permission to reproduce some of the photographs of Bedford material included in her monograph on Antarctic archaeocyathids.

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—— 1961. See under Musatov, D. I. *et al.*, 1961.

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—— 1964a. See Below.

ZHURAVLEVA, I. T., KONYUSHOV, K. N. & ROZANOV, A. Yu. 1964. Archaeocyatha of Siberia: The two-walled Archaeocyatha. *Izd. Akad. Nauk SSR*, *Inst. Geol. Geofiz.*, Moscow. **1964** : 166, 16 pls., 75 figs. [In Russian.]

APPENDIX

GLOSSARY

APEX	initial part of cup.
CENTRAL CAVITY	space inside the inner wall.
DISSEPIMENTS	non-skeletal vesicular connections between the septa.
ENDOTHECA	tissue formed on the central cavity side of the inner wall.
EXOTHECA	diverse external outgrowths from the intervallum and outer wall.
INTERSEPT/INTERSEPTUM	space between two adjacent septa.
INTERTABULUM	space between 2 successive tabulae.
INTERVALLUM	space between the inner and outer walls.
LINTEAUX	skeletal elements around the pores.
LOCULUS	space limited by the two walls, two adjacent septa and on occasion by two successive tabulae.
PELLIS	thin calcareous sheath, porous or not, outside the walls of some genera.
PORES	simple perforations in the skeletal elements.
SEPTA	porous, radial vertical plates connecting the inner and outer walls.
SYNAPTICULAE	horizontal rods between 2 neighbouring septa.
TABULAE	straight, or curved; porous, or pectinate plates that cross the intervallum.
TAENIAE	thick, skeletal; irregular, or waved; sometimes gondola-shaped, plates, that radially subdivide the intervallum and are only found in the Irregularia.
TUMULI	wall protuberances.

EXPLANATION OF PLATES

All the figured material is in the collections of the British Museum (Natural History).

PLATE 1

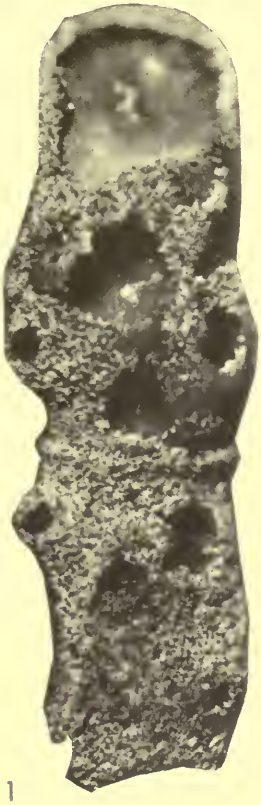
FIG. 1. ***Tumuliolynthus irregularis*** (R. & W. R. Bedford). Holotype S 4141. Outer view of the wall and tumuli. × 15.

FIG. 2. ***Alphacyathus cf. annularis*** R. & W. R. Bedford. S 4822. Etched longitudinal section showing the outer wall, the inner wall and the horizontal rods. × 15.

FIG. 3. ***Monocyathus porosus*** R. & W. R. Bedford. Lectotype S 4140. Cup showing outer view of the wall. × 6.

FIG. 4. ***Monocyathus mellifer*** R. & W. R. Bedford. S 4821. Outer view of the wall. × 6.

FIG. 5. ***Archaeocyathellus*** (***Stapicyathus***) ***stapipora*** (Taylor). S 4733. Detail of inner wall. × 25.



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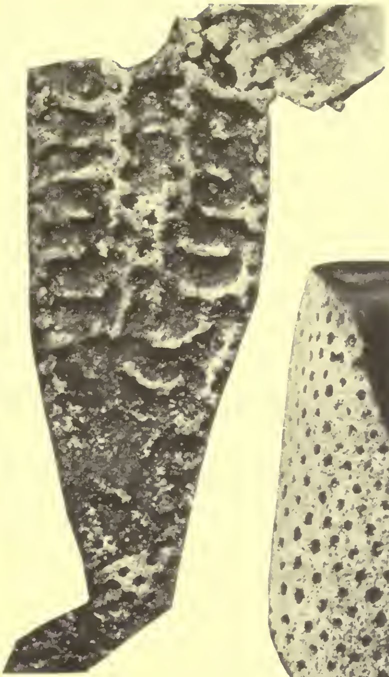

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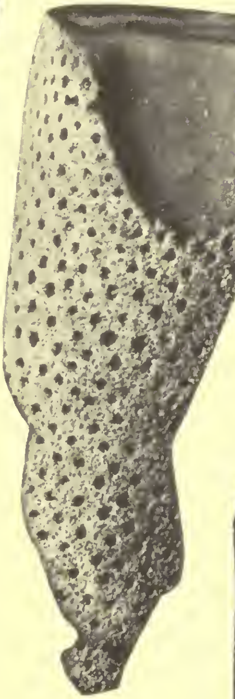

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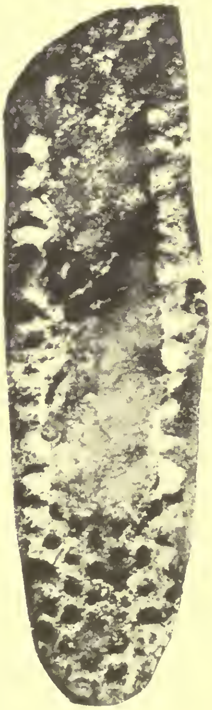

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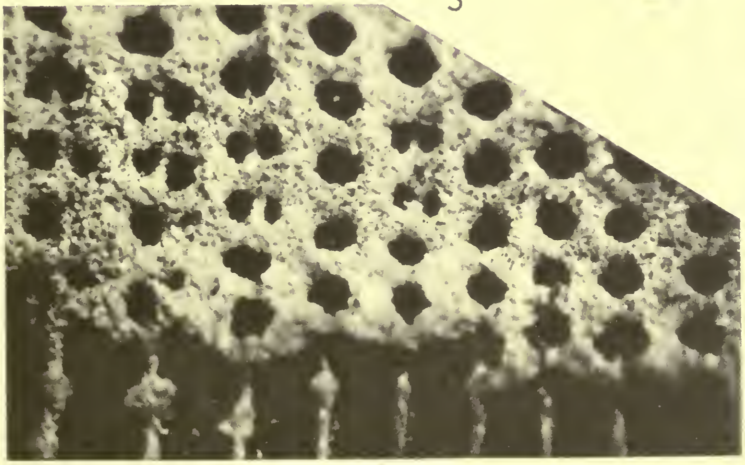


PLATE 2

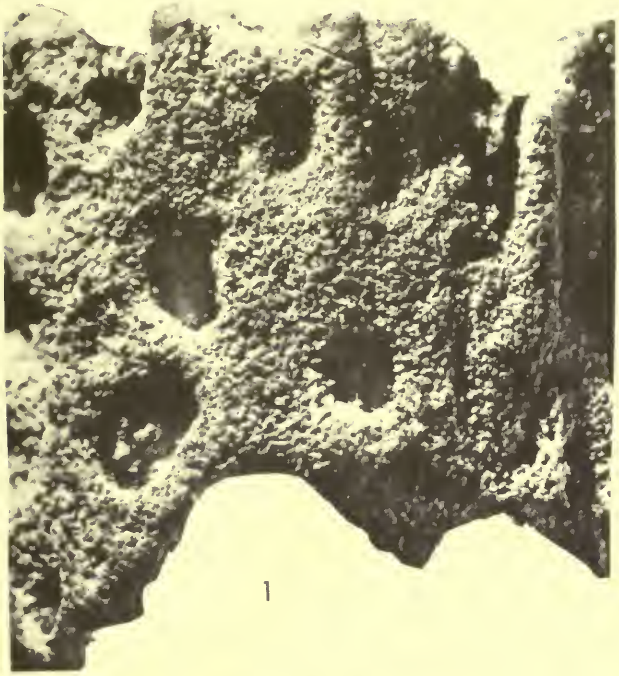
Acanthinocyathus apertus R. & W. R. Bedford

Fig. 1. Paratype S 4167. View of part of outer wall showing pores and position of spines. × 10 approx.

Fig. 2. Paratype S 4167. View of part of outer wall showing lateral view of a spine. × 6 approx.

Fig. 3. Holotype S 4166. Another view of outer wall showing the occurrence of the spines. × 10 approx.

Fig. 4. Paratype S 4168. View of inner wall. × 4.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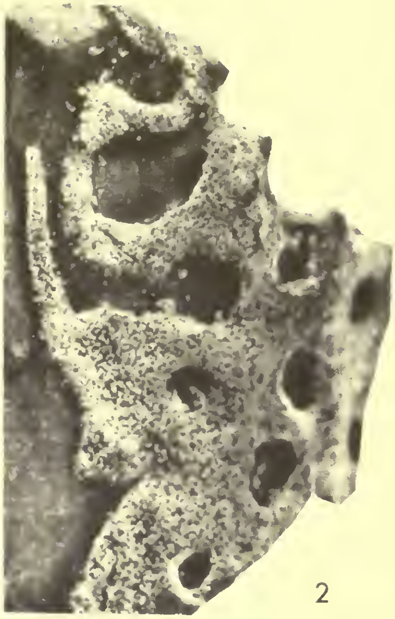
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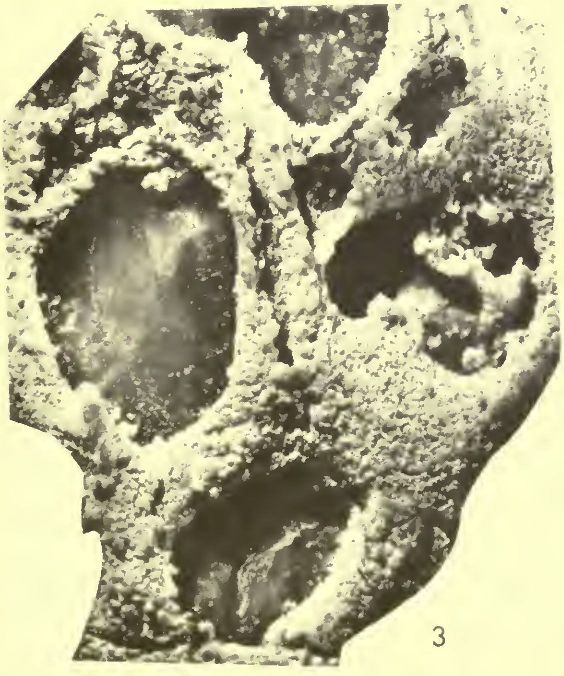
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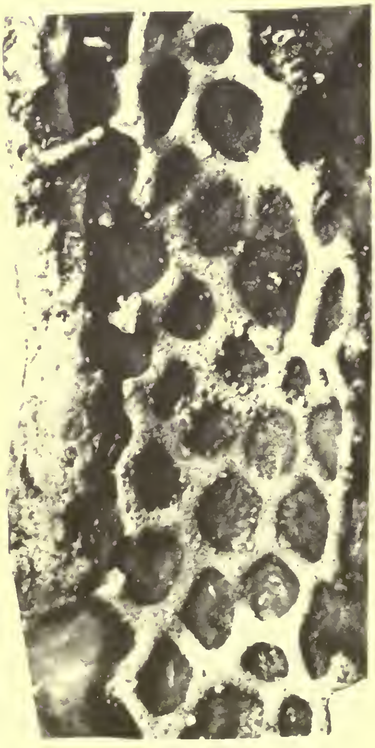
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PLATE 3

Loculicyathus* (*Loculicyathellus*) *floreus (R. & W. R. Bedford)

Holotype S 4144.

Fig. 1. Inner wall and inner part of septa. × 10.
Fig. 2. Outer wall on two intersepts. × 10.
Fig. 4. Upper transverse section. × 10.

Ethmocoscinus papillipora (R. & W. R. Bedford)

Holotype S 4164.

Fig. 3. Part of transverse section. × 15.

Robustocyathus magnipora (R. & W. R. Bedford)

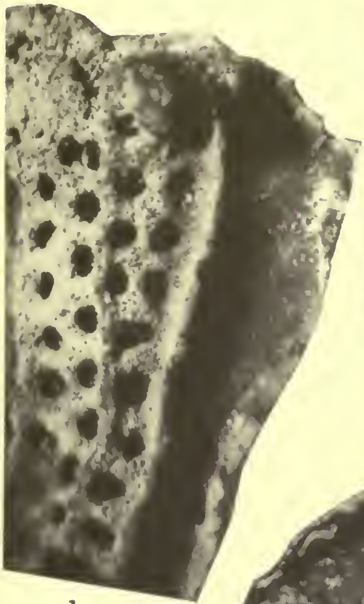
Holotype S 4146.

Fig. 5. Inner wall, septa and outer wall seen from the central cavity. × 5.

Robustocyathus subacutus (R. & W. R. Bedford)

Holotype S 4142.

Fig. 6. Transverse section. × 5.
Fig. 7. View from central cavity of inner wall, septa. × 5.



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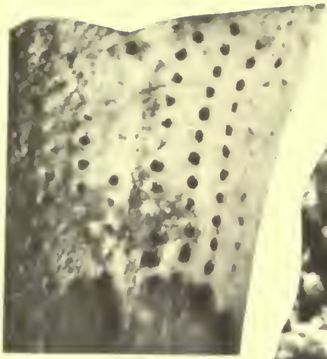

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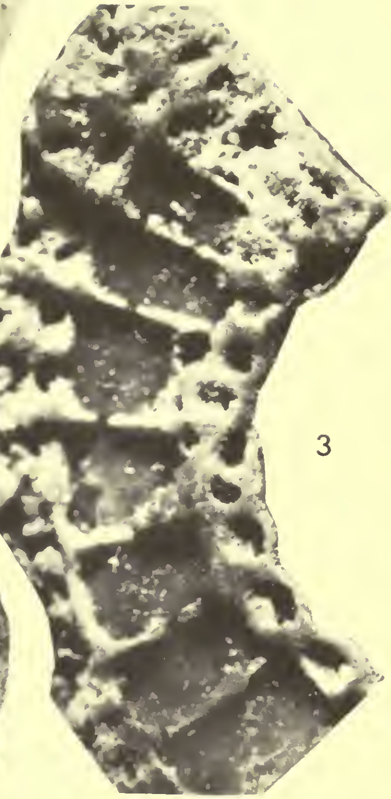

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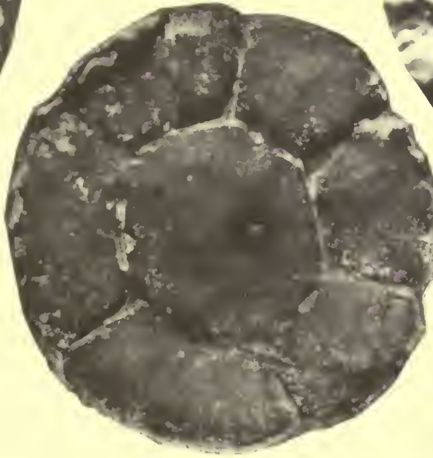

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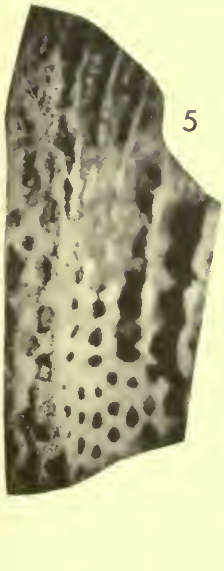

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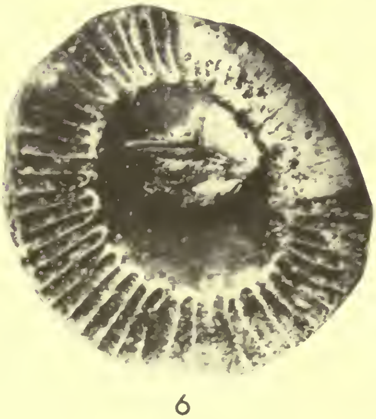

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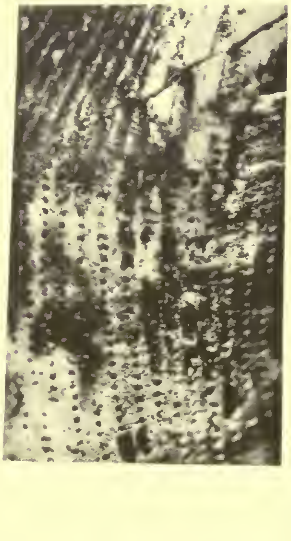

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PLATE 4

Zonacyathus retezona (Taylor)

Fig. 1. S 4731. Detail of inner wall. ×12·5.
Fig. 2. S 4764. Oblique transverse section. ×6.
Fig. 3. S 4353. Etched longitudinal section showing inner wall, septa and outer wall. ×6.

Zonacyathus retevallum (R. & W. R. Bedford)

Fig. 4. Holotype S 4147. Detail of inner wall. ×15.
Fig. 5. S 4726. Transverse section. ×6.

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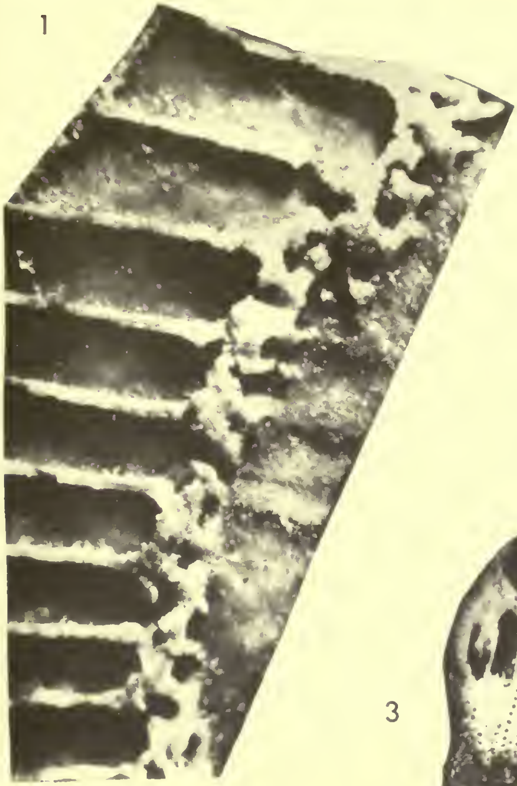

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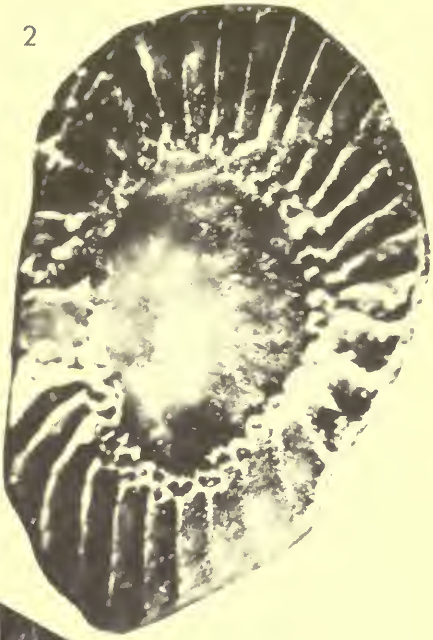

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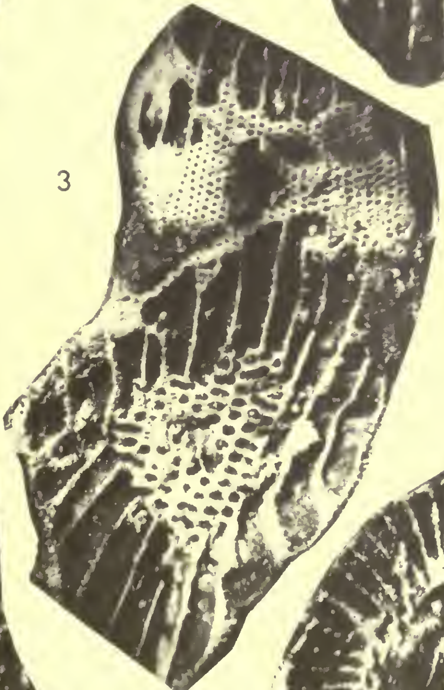

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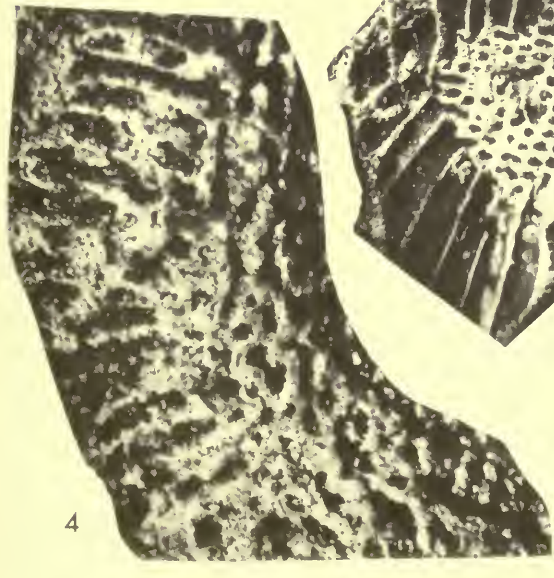

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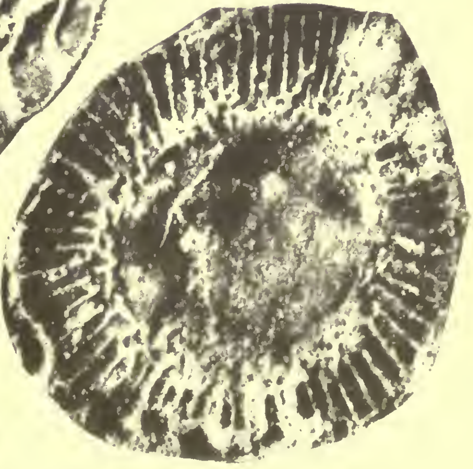

PLATE 5

Ethmocyathus lineatus R. & W. R. Bedford

Holotype S 4149.

FIG. 1. Detail of inner wall showing lozenge pores and tabellae. × 10.
FIG. 2. Porosity of septa. × 25.
FIG. 3. Inner view of outer wall. × 40.

Cyathocricus tracheodentatus R. & W. R. Bedford

Holotype S 4148.

FIG. 4. Lower transverse section. × 6.
FIG. 5. Etched longitudinal section showing the inner wall. × 6.

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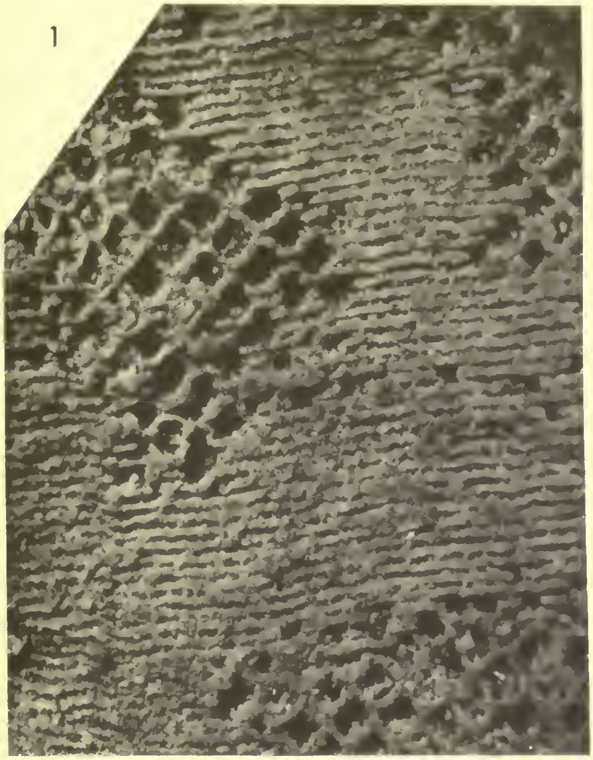

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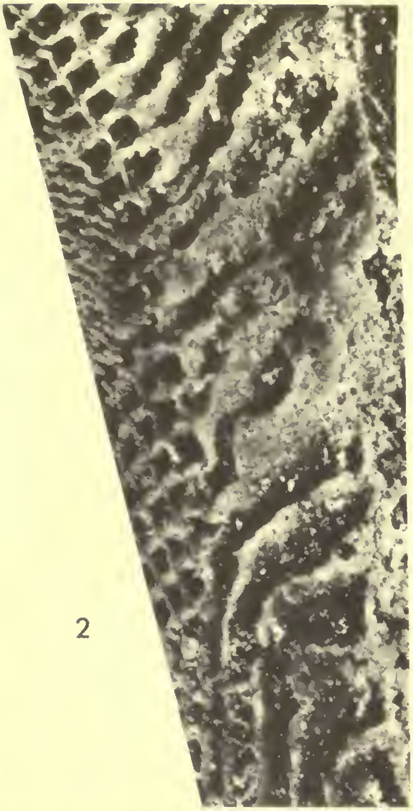

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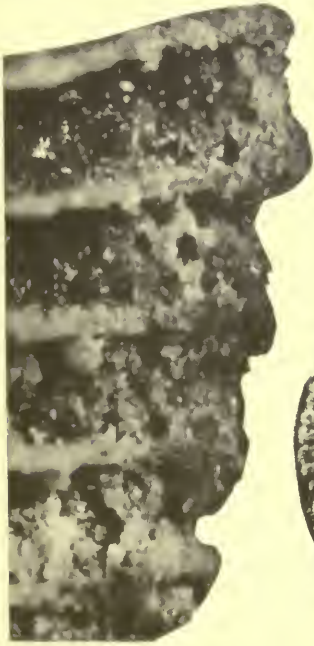

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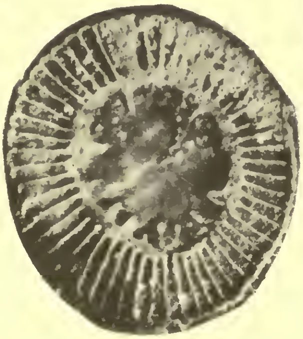

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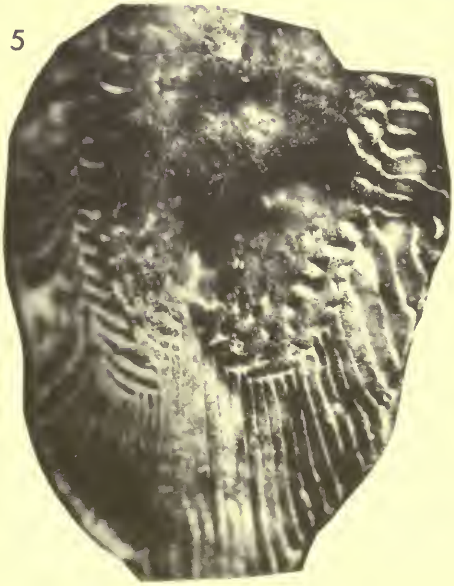


PLATE 6

Cyathocricus dentatus (Taylor)

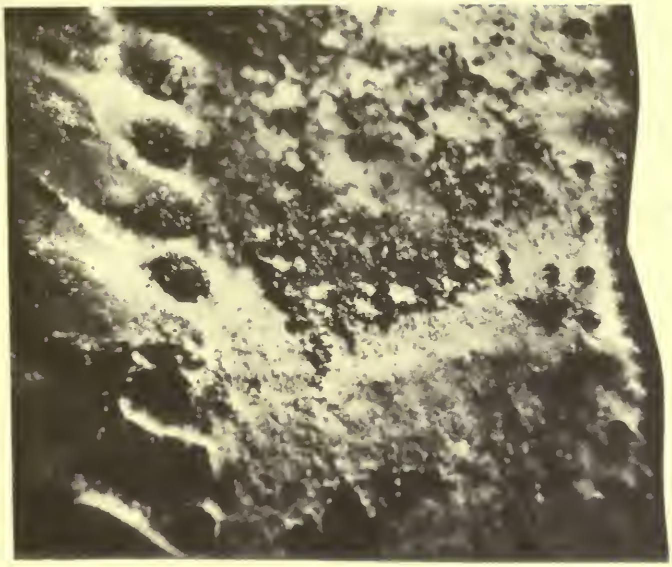
FIG. 1. S 4753. Longitudinal section showing the rings and teeth (note that the septa are only porous near the outer wall) and outer wall. ×30.

FIG. 2. S 4753. Etched transverse section. ×10.

FIG. 3. S 4355. Etched longitudinal section showing the outer wall, the septa and the inner wall (at the upper part of the figure). ×8.

Cyathocricus tracheodentatus (R. & W. R. Bedford)

FIG. 4. S 4754. Detail of inner wall. ×25.



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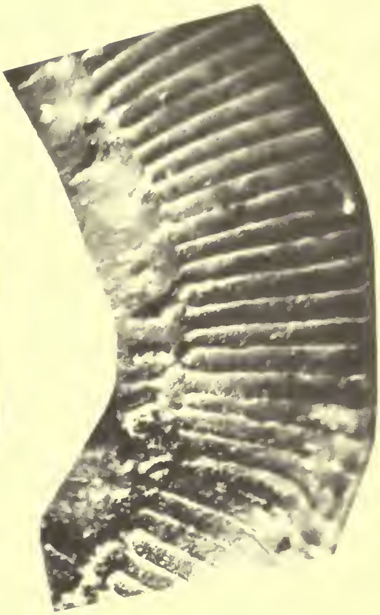

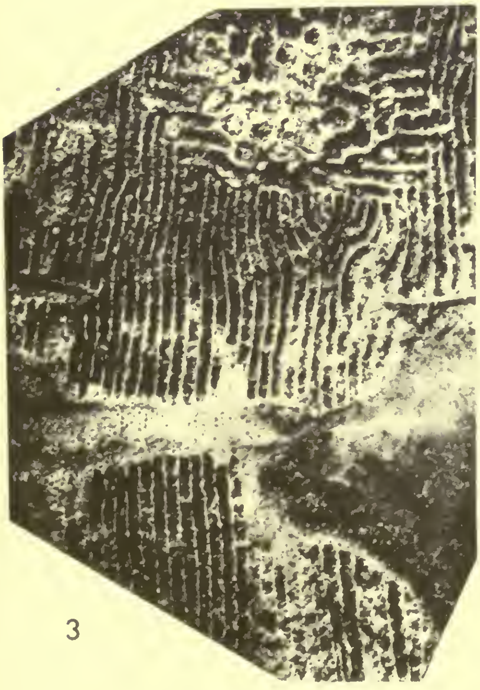

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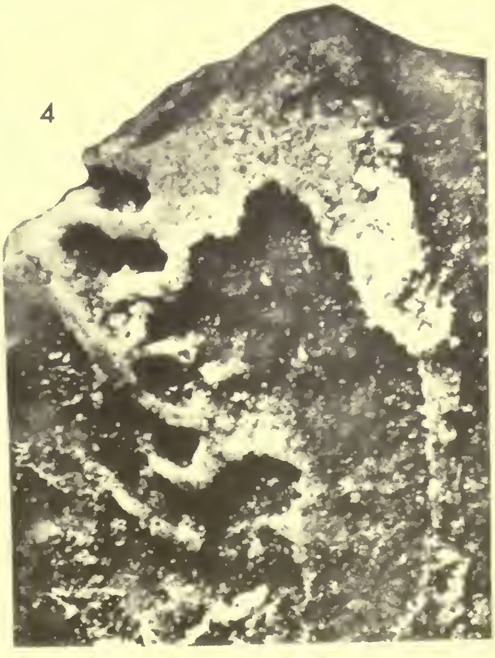


PLATE 7

Erismacoscinus equivallum (Taylor)

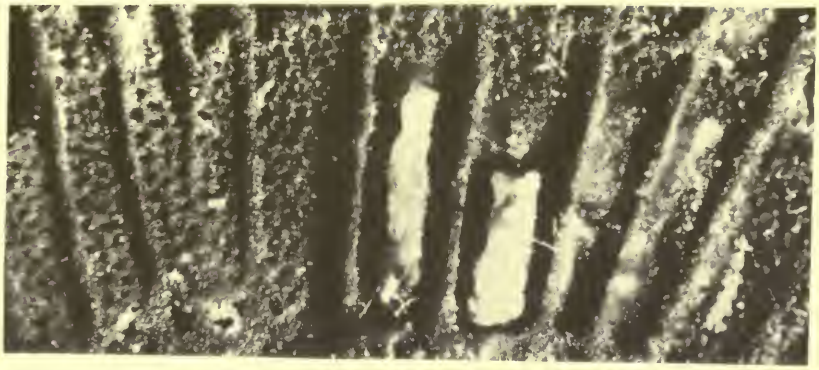
Holotype S 198.

FIG. 1. Detail of one tabula [on opposite side to Fig. 2]. × 15.
FIG. 2. Transverse section showing inner wall pores and tabula. × 3.
FIG. 3. Detail of outer wall. × 8.
FIG. 5. Detail of inner wall. × 15.

Erismacoscinus quadratus (R. & W. R. Bedford)

Holotype S 4157.

FIG. 4. Etched oblique longitudinal section. × 5.



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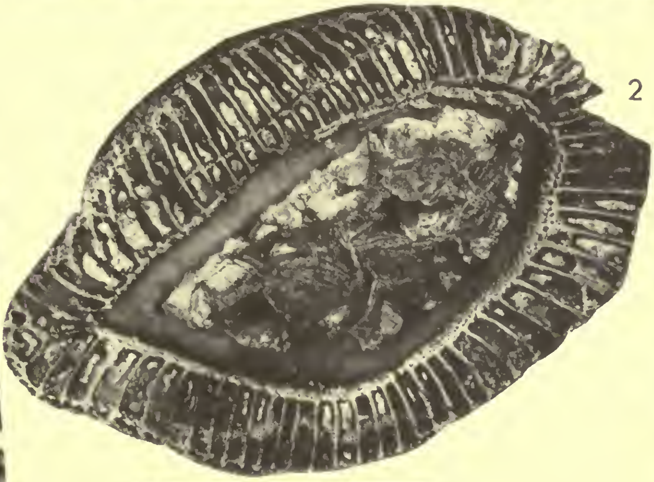

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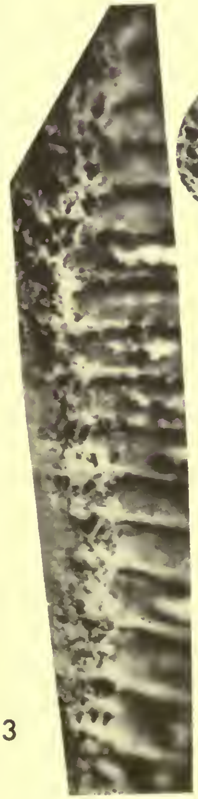

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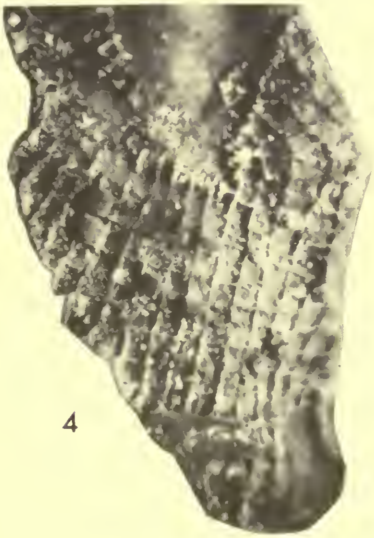

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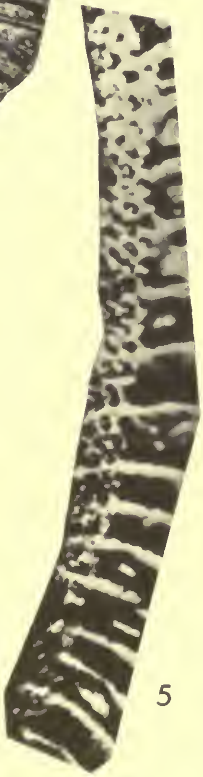

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PLATE 8

Erismacoscinus cellularis (R. & W. R. Bedford)

Holotype S 4162.

FIG. 1. Detail of septa and inner wall (on right). × 15.

FIG. 4. Oblique transverse section. × 6.

Erismacoscinus rugosus (R. & W. R. Bedford)

Holotype S 4152.

FIG. 2. Outer view of outer wall. × 10.
FIG. 3. Oblique longitudinal section. × 10.

Erismacoscinus quadratus (R. & W. R. Bedford)

FIG. 5. Holotype S 4157. Transverse section and detail of the inner wall. × 10.

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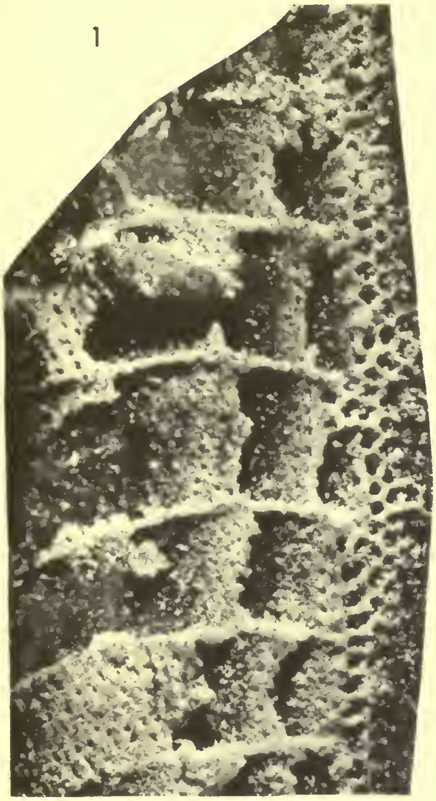

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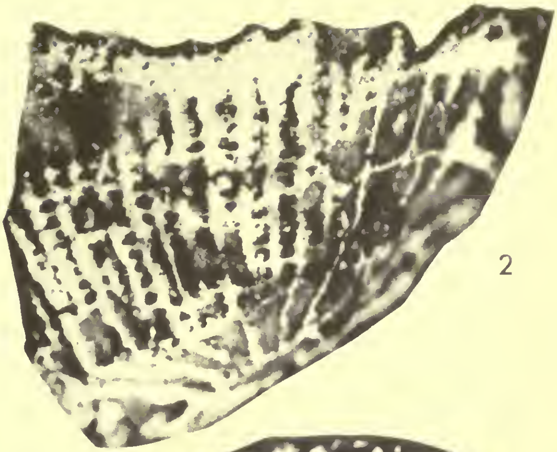

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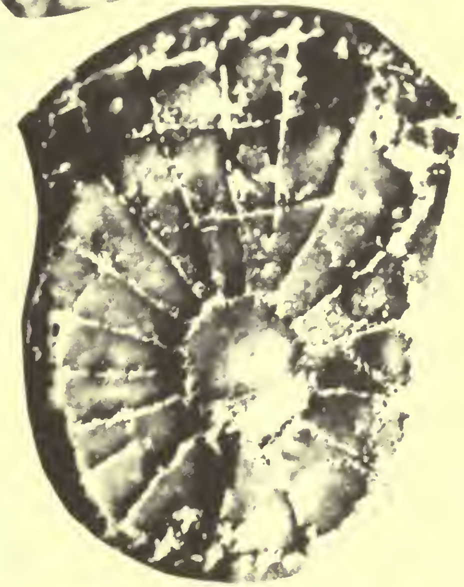

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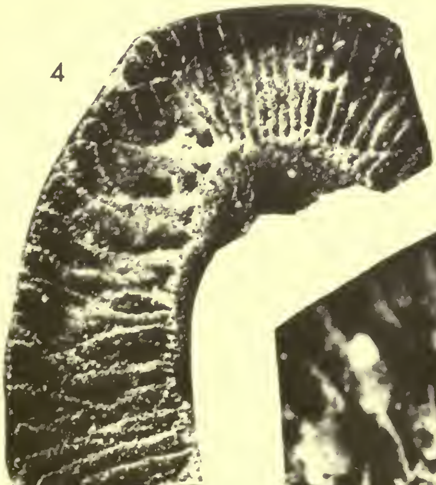

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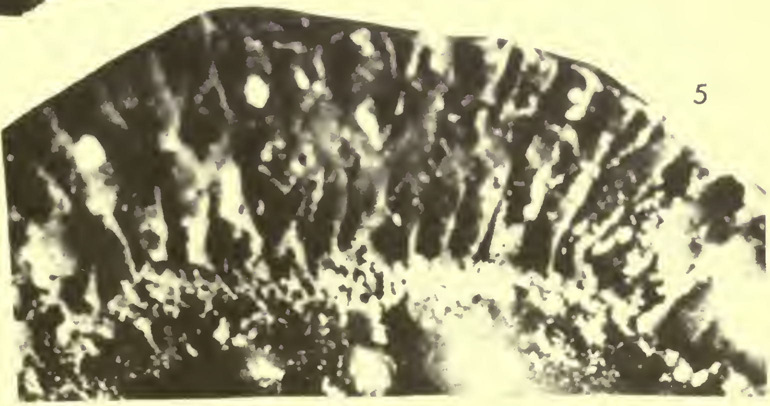


PLATE 9

Erismacoscinus textilis (R. & W. R. Bedford)

Paratype S 4156.

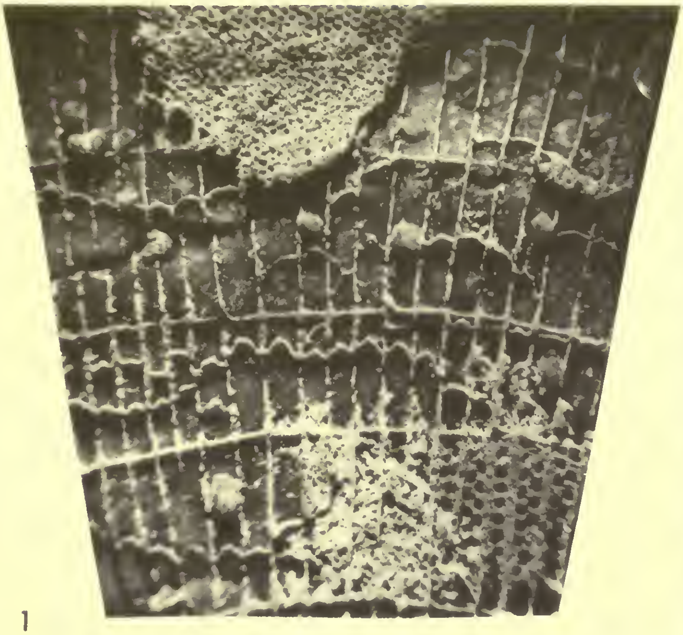
FIG. 1. Detail of outer wall (lower right), septa, tabulae, vesicular tissue (centre) and inner wall (above left). ×6.

FIG. 3. Bowl shape. ×1·5.

Holotype S 4155.

FIG. 2. Cylindrical shape. ×4.

FIG. 4. Transverse section. ×5.



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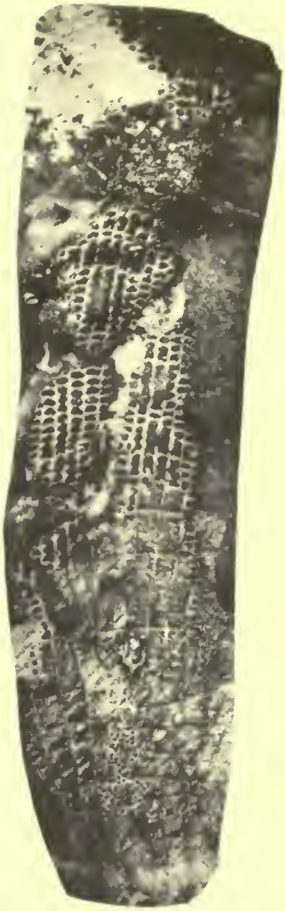

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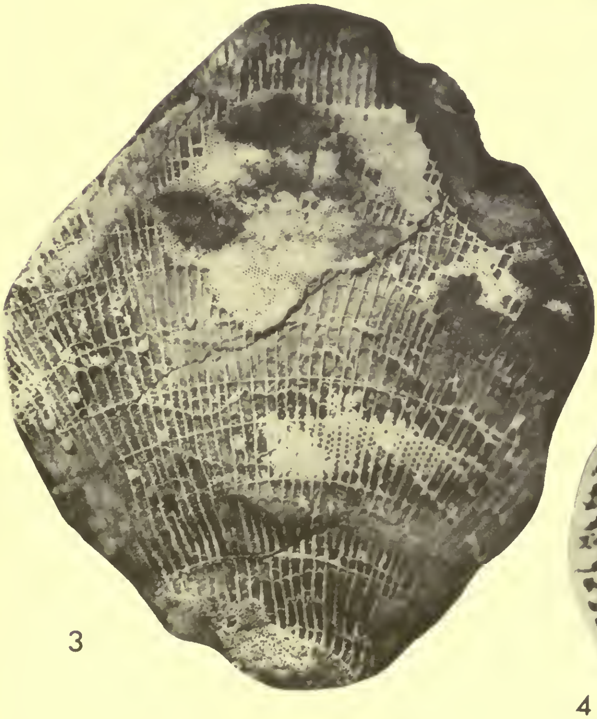

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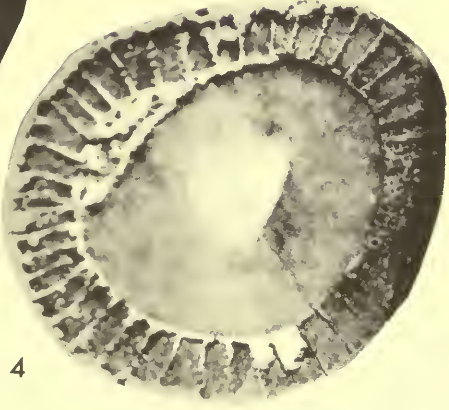

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PLATE 10

Alataucyathus* (*Anaptyctocyathus*) *flabellus sp. nov.

Holotype S 4161.

FIG. 1. Outer view. × 2.

Erismacoscinus retifer (R. & W. R. Bedford)

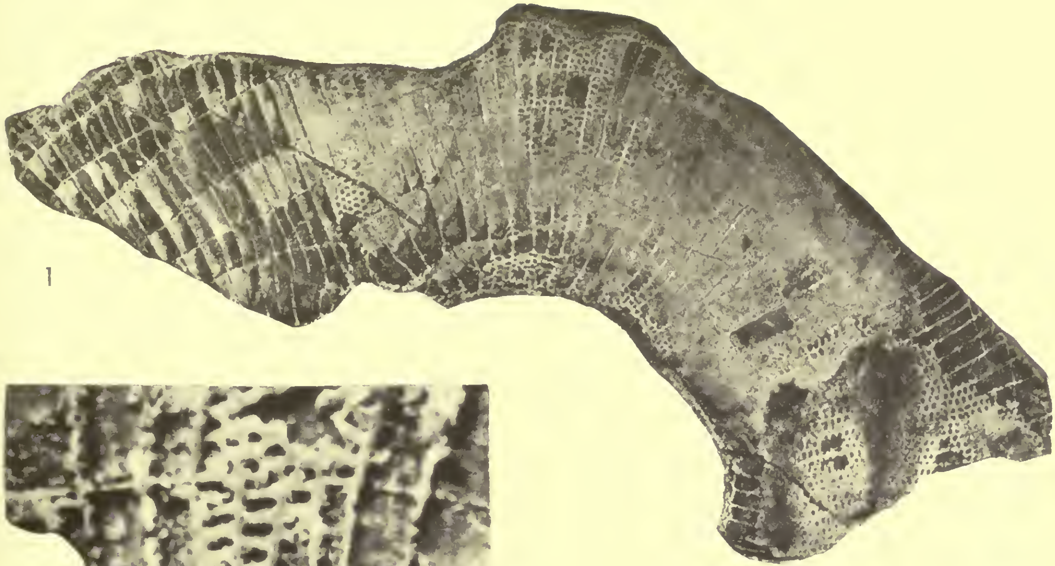
Holotype S 4159.

FIG. 2. Etched inner wall seen from central cavity. × 10.
FIG. 3. Transverse section. × 5.

Erismacoscinus petersi (R. & W. R. Bedford)

Holotype S 4158.

FIG. 4. Transverse section. × 10.
FIG. 5. Longitudinal section. × 10.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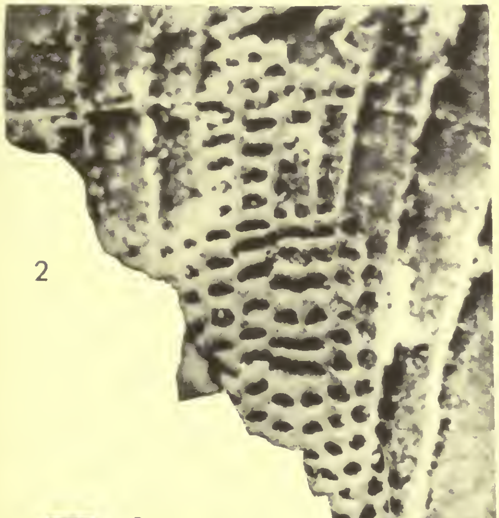
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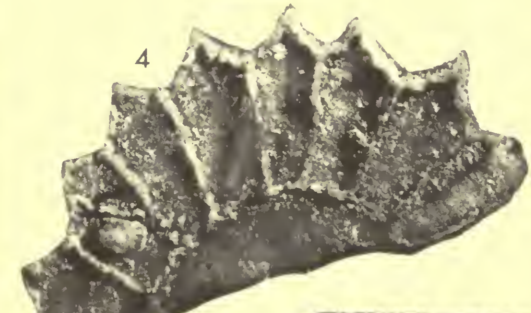
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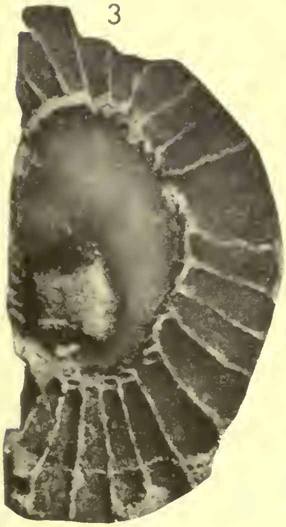
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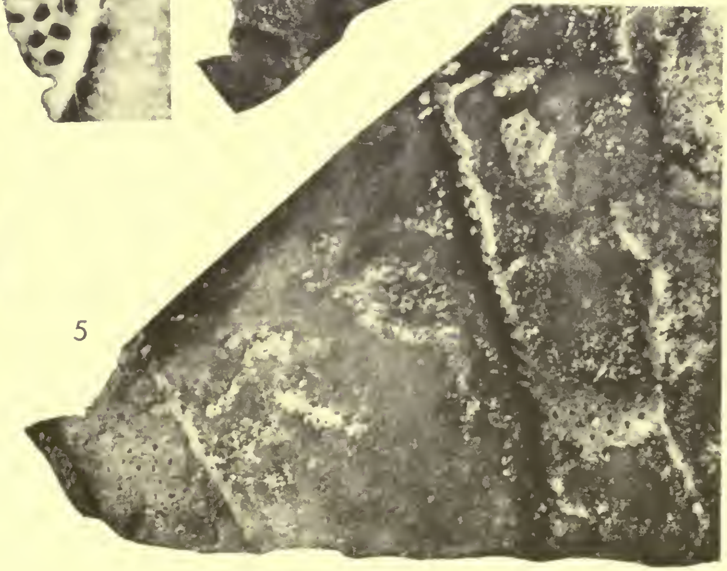
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PLATE 11

Alataucyathus* (*Anaptyctocyathus*) *cribripora (R. & W. R. Bedford)

Holotype S 4160.

FIG. 1. Detail of outer wall, external view of pores and micropores. × 25.
FIG. 3. Longitudinal section. × 10.

Tomocyathus* (*Erugatocyathus*) *papillatus (R. & W. R. Bedford)

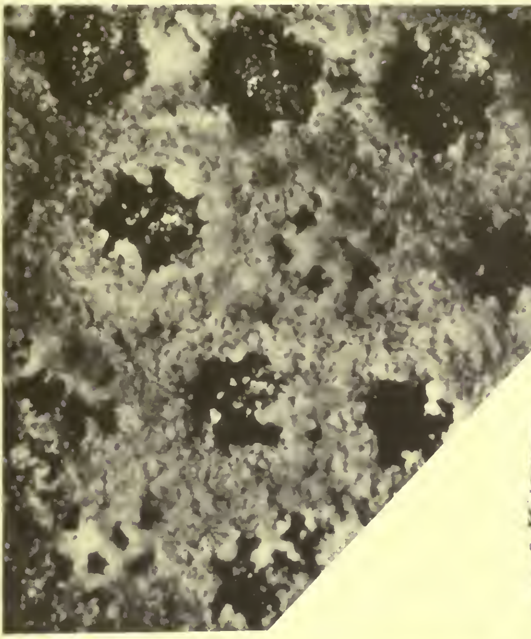
Holotype S 4153.

FIG. 2. Upper transverse section. × 5.

Salairocyathus* (*Salairocyathus*) *annulatus (R. & W. R. Bedford)

Holotype S 4163.

FIG. 4. Detailed longitudinal section showing the inner wall. × 5.



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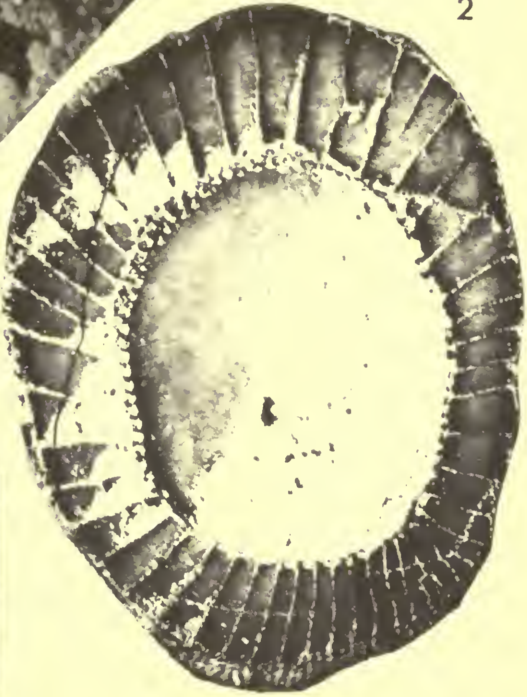

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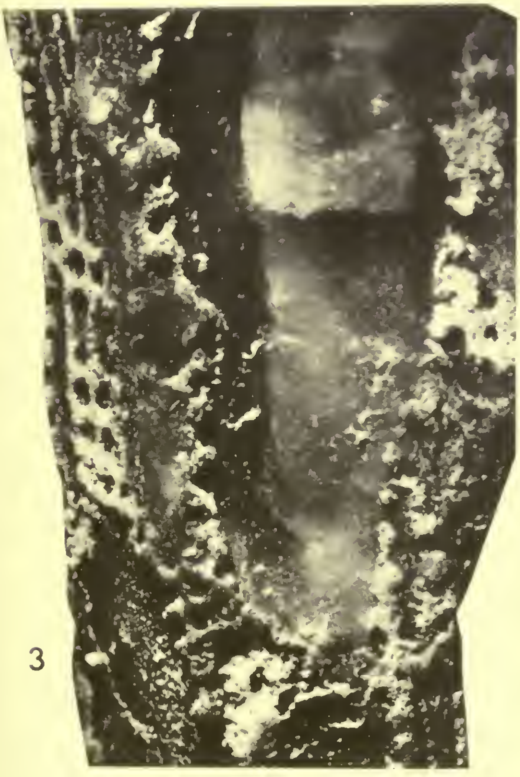

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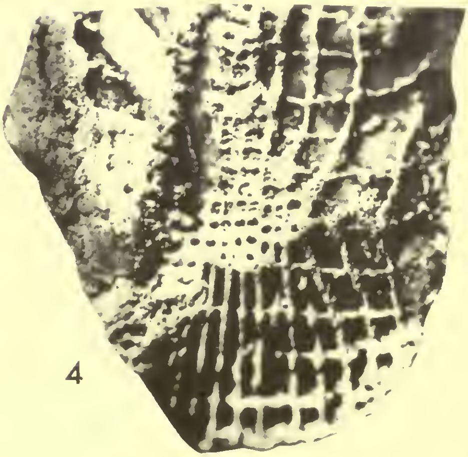

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PLATE 12

Pinacocyathus spicularis R. & W. R. Bedford

Holotype S 4169

FIG. 1. Transverse section. ×7.

FIG. 2. Outer view showing the scaffolding of rods. ×7.

Flindersicyathus (**_Flindersicyathus_**) **_graphicus_** (R. & W. R. Bedford)

FIG. 3. Paratype S 4171. Longitudinal section through an unwaved taenia (with central cavity to the left). × 6.

FIG. 4. Paratype S 4171. Longitudinal section showing an inner view of the inner wall. ×6.

FIG. 5. Holotype S 4170. Transverse section. ×6.

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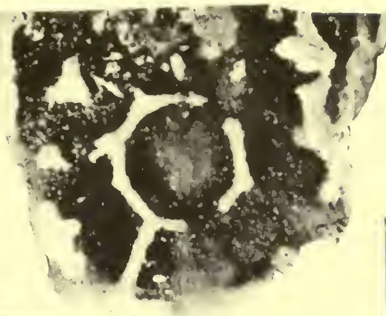

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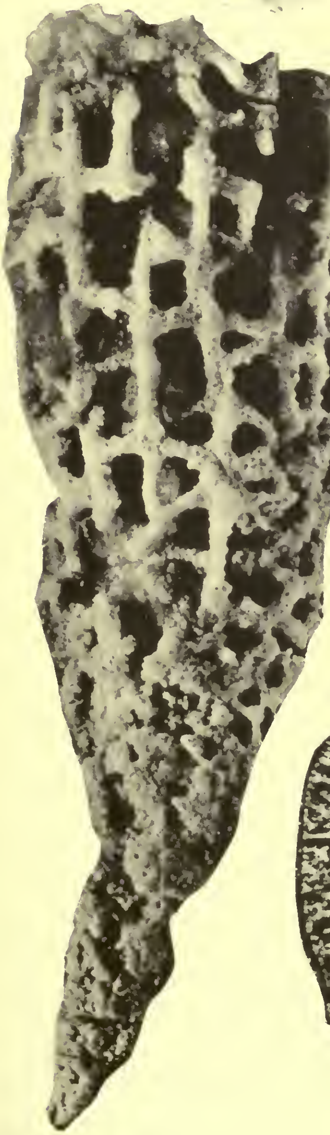

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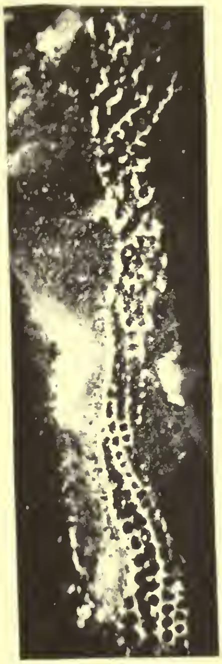

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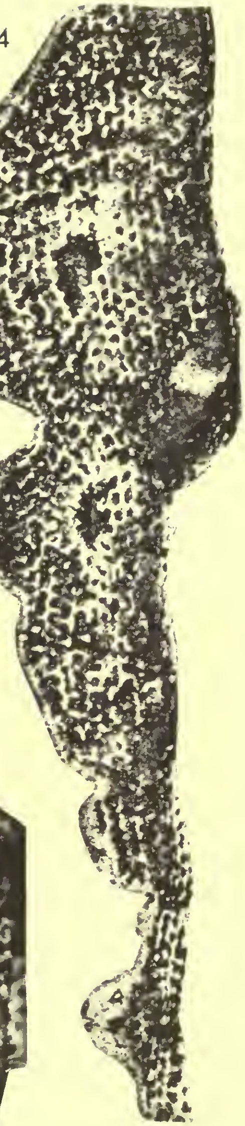

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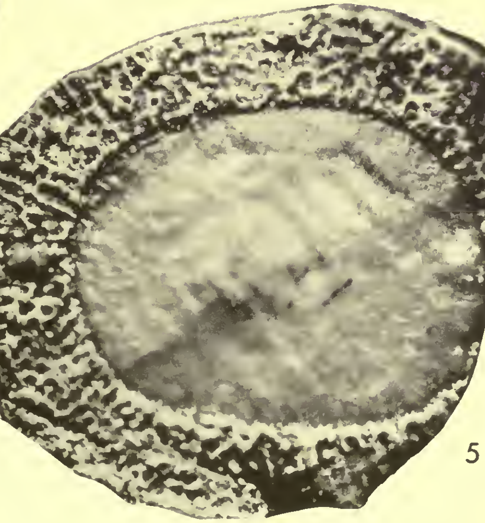


PLATE 13

Metaldetes taylori (R. & W. R. Bedford)

Holotype S 4185–4187 (three pieces of the same specimen)

FIG. 1. S 4185. Lower part; external view. ×2·2 approx.

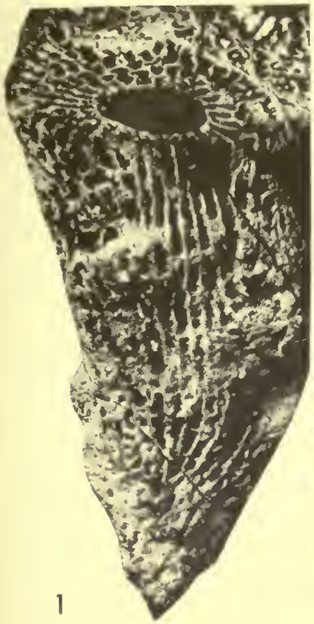
FIG. 2. S 4186. Upper part; transverse section. ×1·8.

FIG. 3. S 4186. Upper part; oblique and longitudinal sections with the septa running N–S. ×2 approx.

These photographs are used by courtesy of the British Museum (Nat. Hist.) and Dr. Dorothy Hill.

?**Coscinocyathus unilinearis** (R. & W. R. Bedford)

FIG. 4. Holotype S 4165. View of both inner and outer walls and intervallum. × 5.



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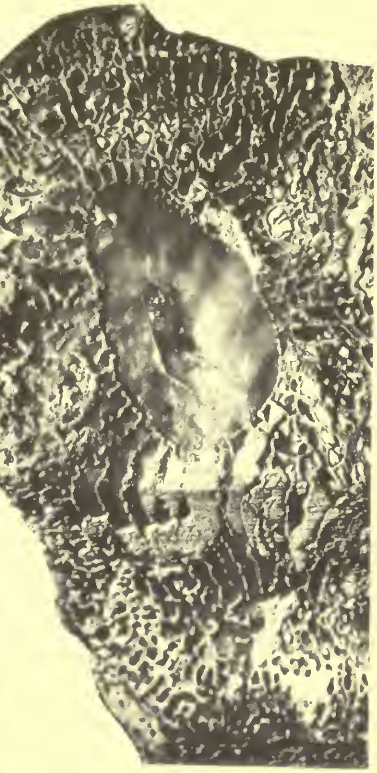

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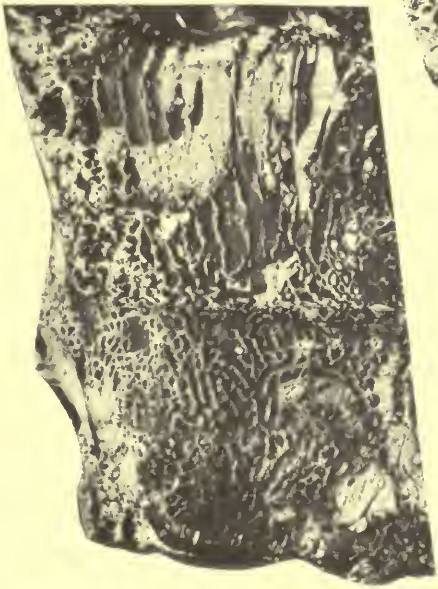

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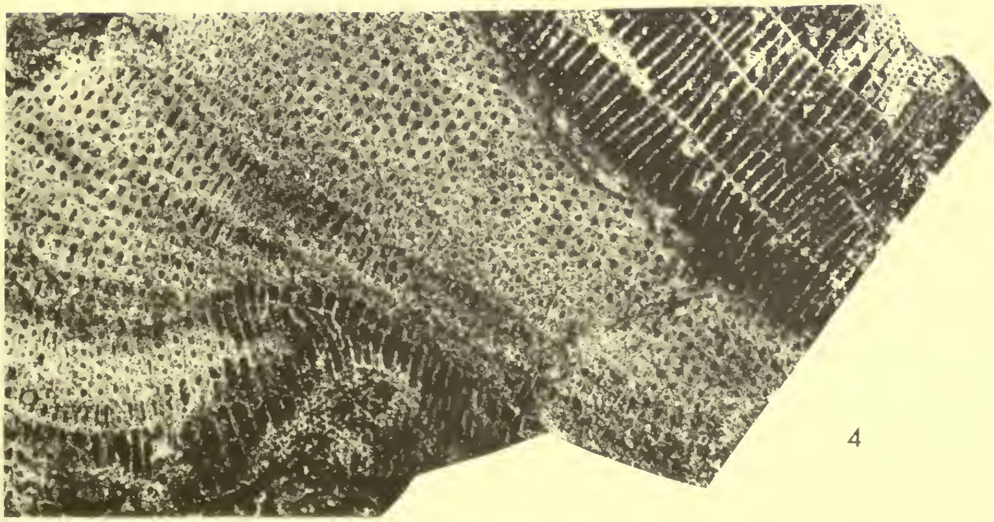

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PLATE 14

Flindersicyathus* (*F.*) *speciosus (R. & W. R. Bedford)

Holotype S 4175.

FIG. 1. Lower transverse section. ×5.

FIG. 3. Etched longitudinal section showing inner wall tubes. ×5.

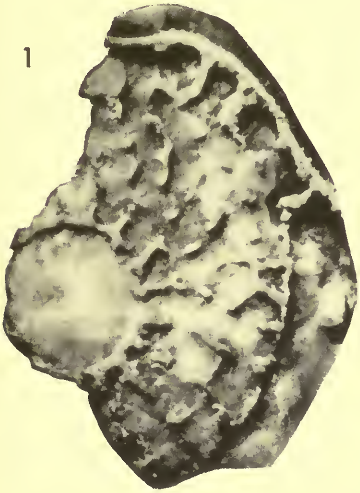
Flindersicyathus* (*F.*) *major (R. & W. R. Bedford)

FIG. 2. Holotype S 4174. Etched longitudinal section showing the bending of flat taeniae (on right) and the widened tubes of the inner wall (on left). ×6.

Flindersicyathus* (*F.*) *irregularis (Taylor)

FIG. 4. S 4763. Part of transverse section showing thickened inner side of taenia. × 10.

1



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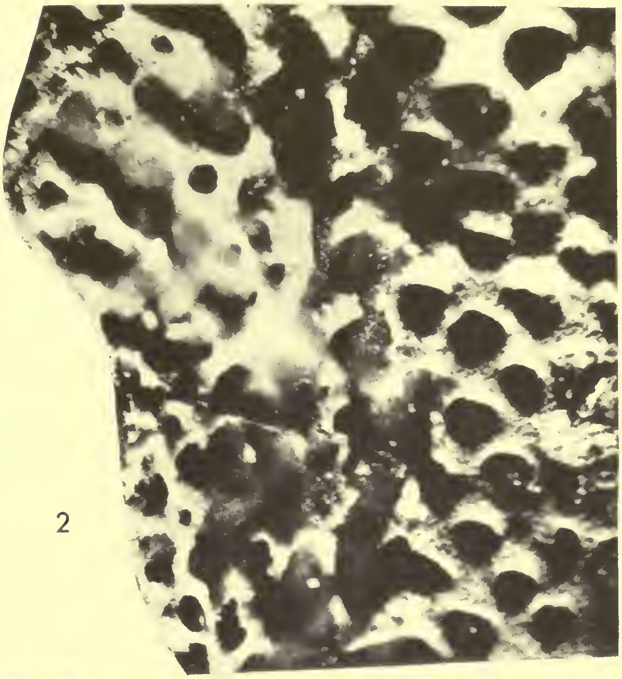

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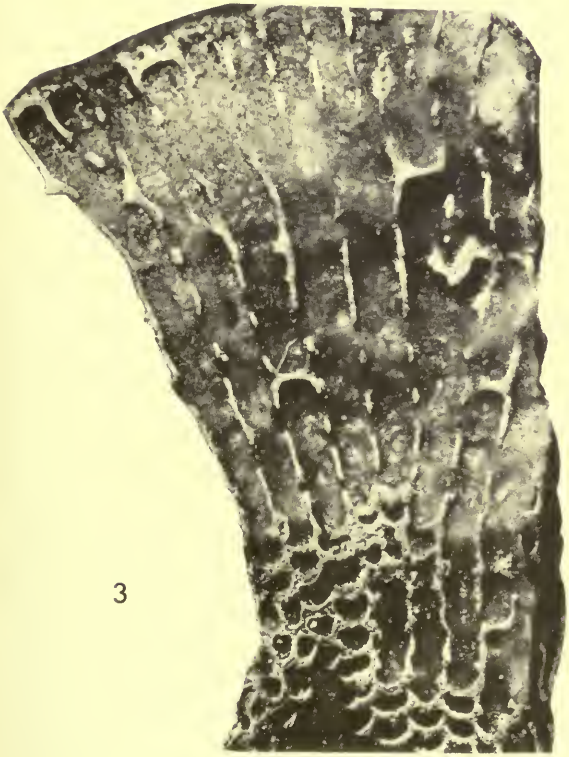

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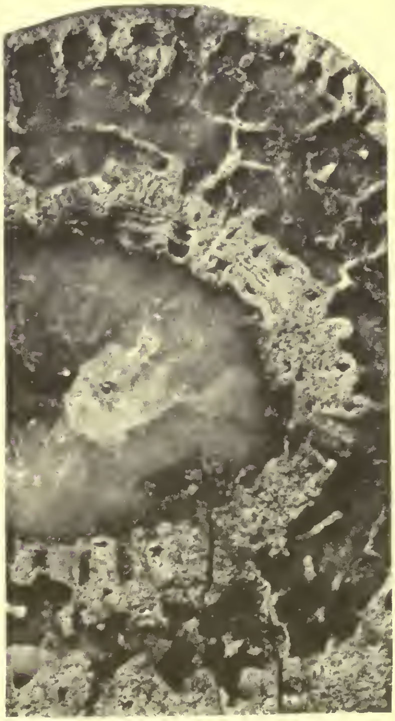

PLATE 15

FIG. 1. ***Flindersicyathus*** (***Pycnoidocyathus***) ***synapticulosus*** (Taylor) S 208. Part of transverse section. × 2·5.

FIG. 2. ***Flindersicyathus*** (***P.***) ***simplex*** (Taylor). Paratype S 4824. Part of longitudinal and transverse sections. × 3.

FIG. 3. ***Flindersicyathus*** (***P.***) ***maximipora*** (R. & W. R. Bedford). Holotype S 4150. Part of an etched longitudinal section showing extended pore-tubes of the inner wall and unwaved taeniae. × 3.

FIG 4. ***Flindersicyathus*** (***P.***) ***vicinisepta*** (R. & W. R. Bedford). S 4825. Part of longitudinal section showing the inner wall. × 5.

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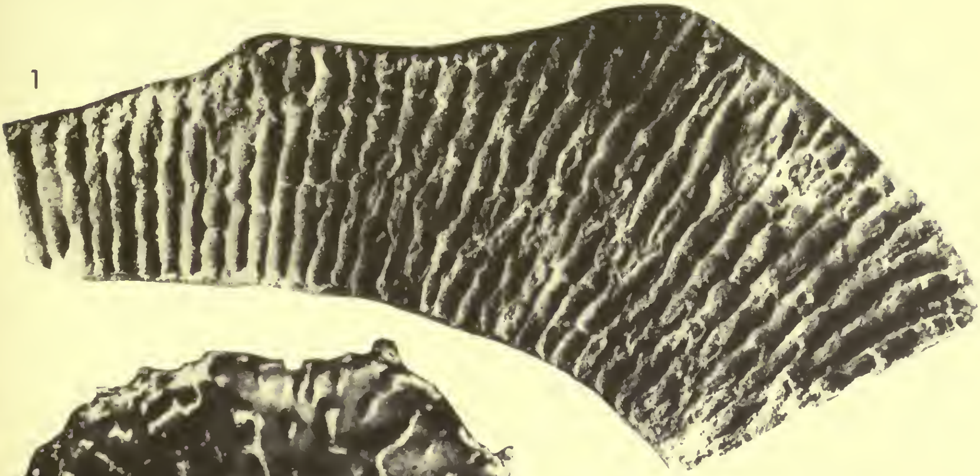

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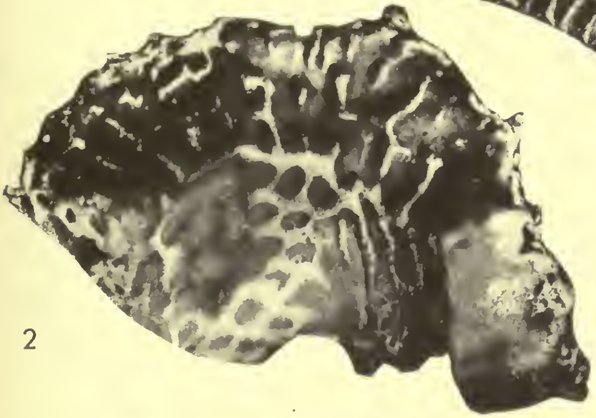

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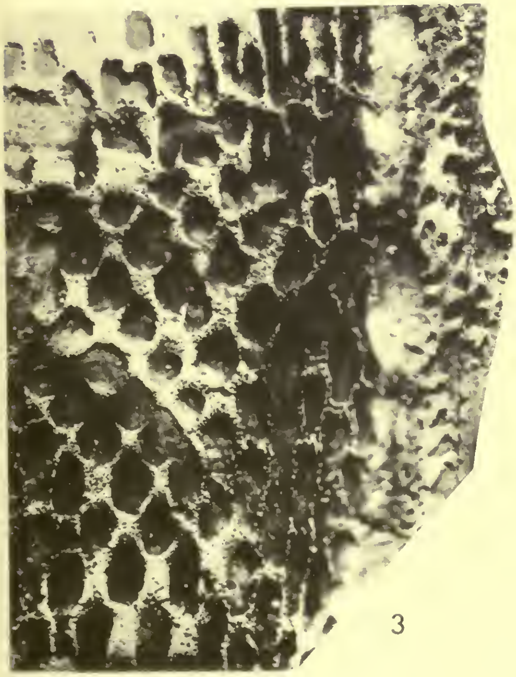

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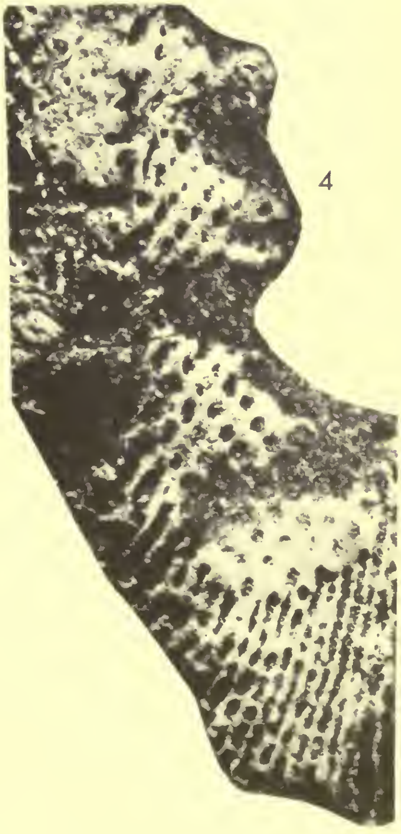


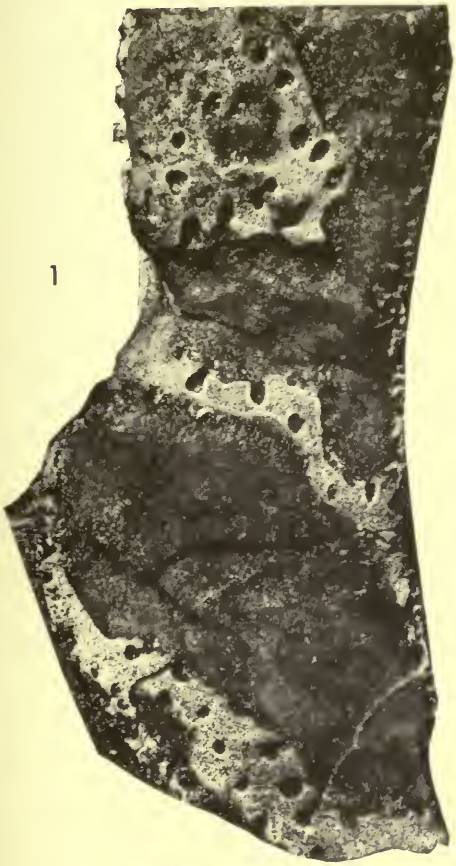
PLATE 16

Metaldetes dissepimentalis (Taylor)

Fig. 1. S 4176. Lateral view of non-waved taeniae. ×6.
Fig. 2. S 4182. Part of transverse section. ×6.
Fig. 3. S 4176. Outer view of outer wall. ×6.

Metaldetes irregularis (R. & W. R. Bedford)

Fig. 4. Paratype S 4190. Outer view of outer wall. ×6.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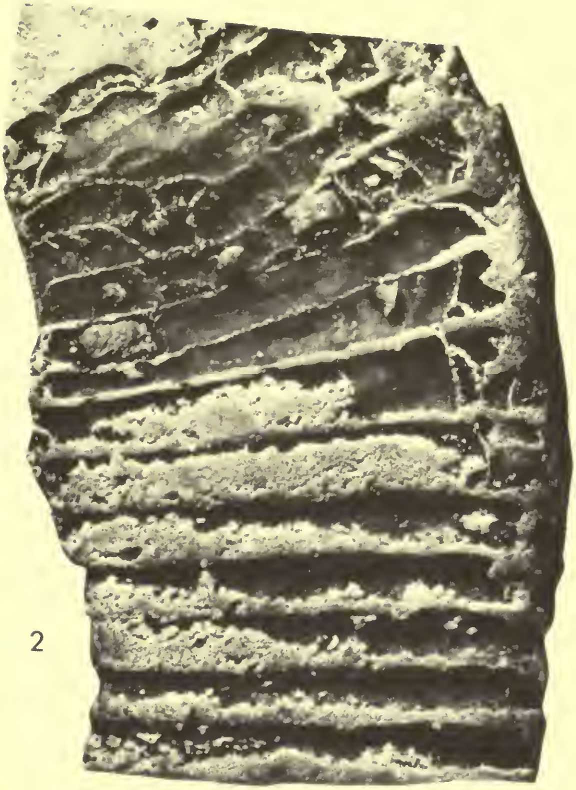
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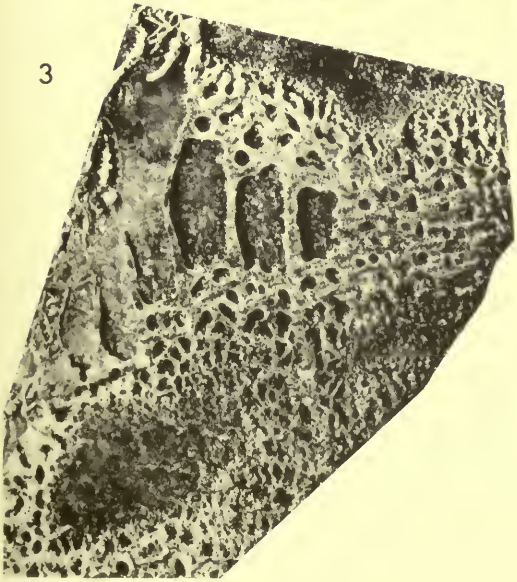
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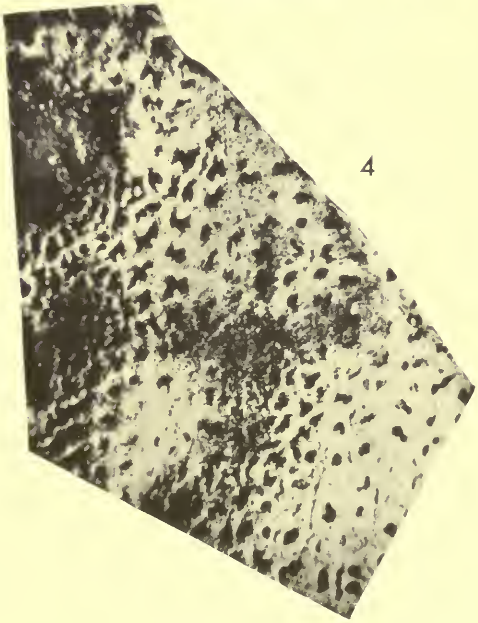
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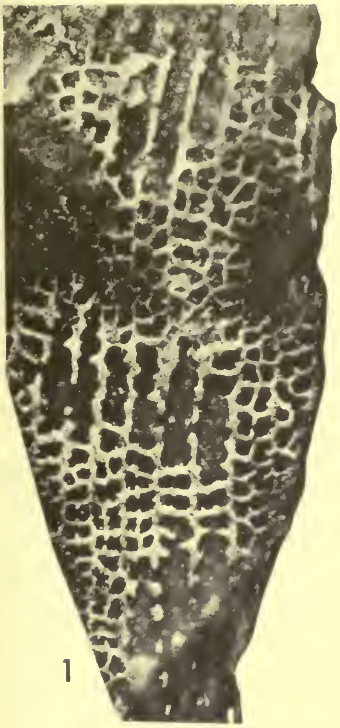
PLATE 17

Metacoscinus reteseptatus R. & W. R. Bedford

FIG. 1. S 4194. Outer view of outer wall. ×6.
FIG. 2. S 4191. Part of transverse section showing a tabula. ×10.
FIG. 3. S 4195. Inner wall seen from the central cavity. ×6.
FIG. 4. S 4194. Section along a taenia (central cavity on left). ×6.



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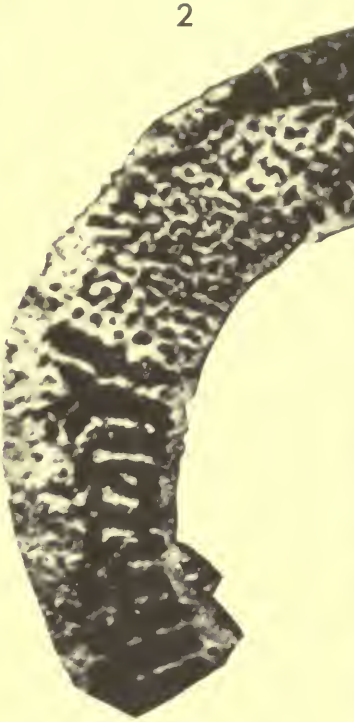

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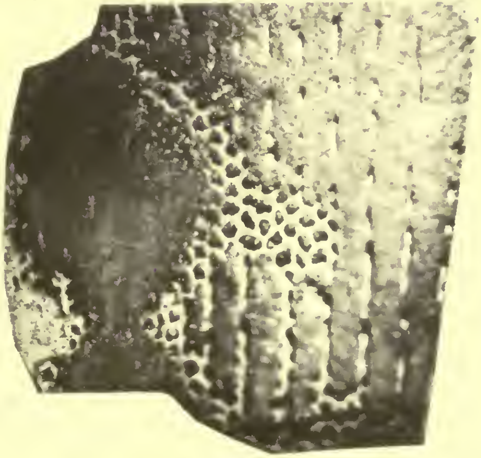

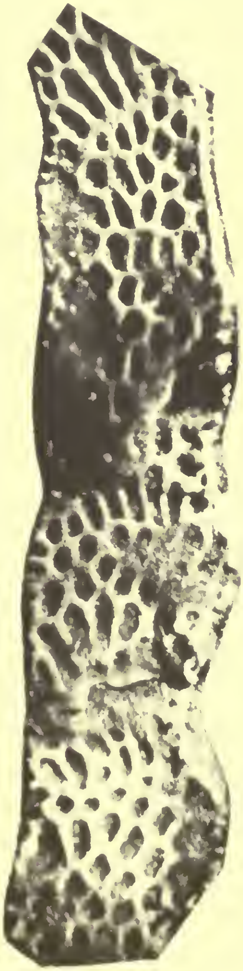

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PLATE 18

Metafungia reticulata R. & W. R. Bedford

Holotype S 4184.

FIG. 1. Inner wall of cup (on left). ×4.
FIG. 2. Outer wall. ×6.
FIG. 3. Transverse section. ×3.

Photographs by courtesy of the British Museum (Nat. Hist.) and Dr. Dorothy Hill.

Pycnoidocoscinus pycnoideum R. & W. R. Bedford

S 4832.

FIG. 4. Part of transverse section showing thickened taeniae. ×5.
FIG. 5. Longitudinal section showing inner wall. ×5.
FIG. 6. Section showing area of fig. 7. ×5.
FIG. 7. Detail of tabulae pores. ×30.
FIG. 8. Detail of taeniae and tabulae. ×30.

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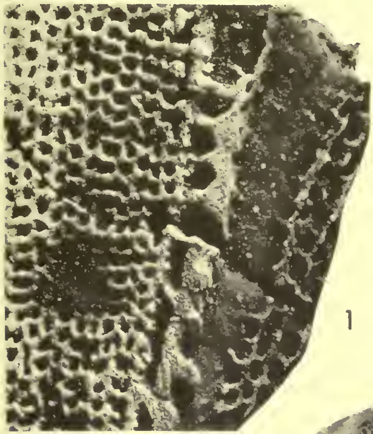
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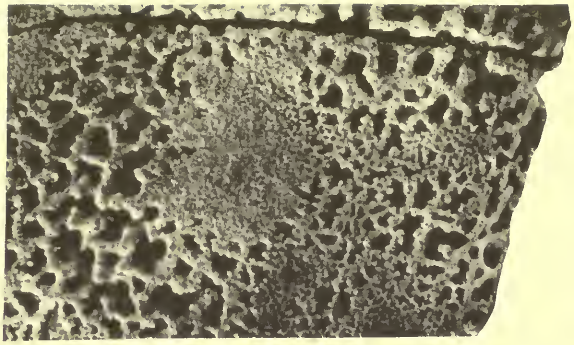
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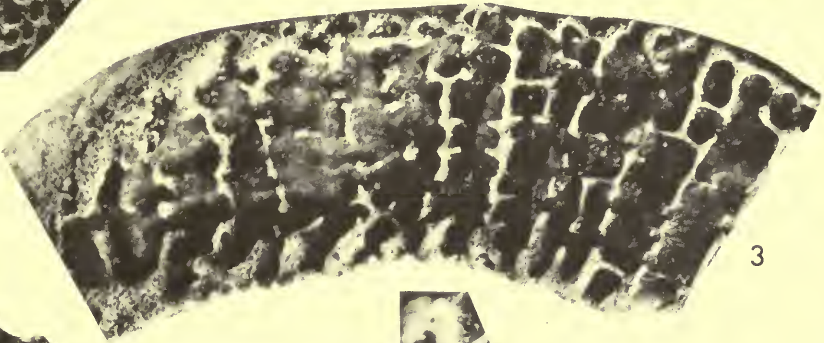
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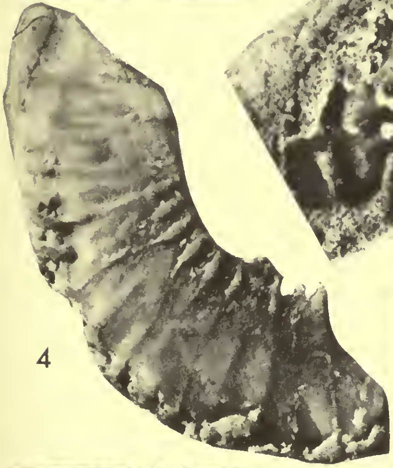
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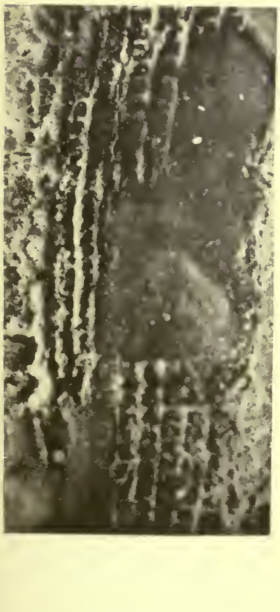
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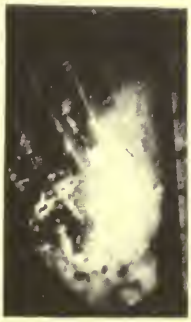
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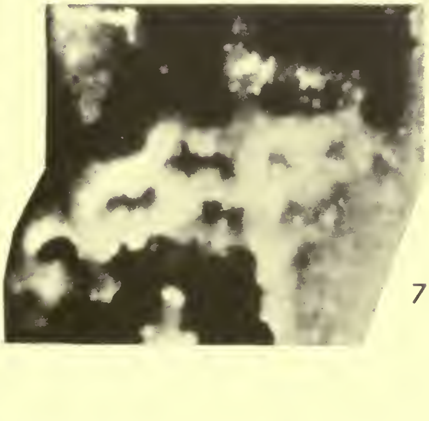
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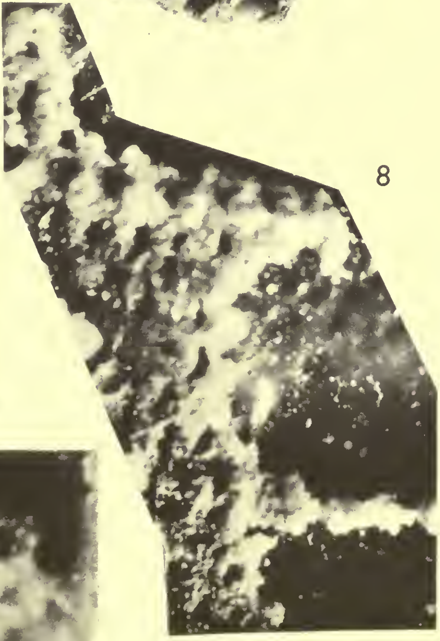
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SOME BATHONIAN OSTRACODA OF ENGLAND WITH A REVISION OF THE JONES 1884 AND JONES & SHERBORN 1888 COLLECTIONS

R. H. BATE

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
GEOLOGY Vol. 17 No. 8

LONDON: 1969

SOME BATHONIAN OSTRACODA OF ENGLAND WITH A REVISION OF THE JONES 1884 AND JONES & SHERBORN 1888 COLLECTIONS

BY

RAYMOND HOLMES BATE

BRITISH MUSEUM
30 MAY 1969
NATURAL HISTORY

Pp. 377–437; 16 *plates*, 18 *text-figures*

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
GEOLOGY Vol. 17 No. 8
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By R. H. BATE

CONTENTS

		Page
I.	Introduction	379
II.	The T. R. Jones Collection	380
III.	The T. R. Jones & C. D. Sherborn and the H. H. Winwood Collections	394
IV.	The J. F. Blake Collection	427
V.	References	435

SYNOPSIS

Three Bathonian ostracod Collections from the Fuller's Earth Clay of Bath, Somerset, and one of similar age (the T. R. Jones Collection, published in 1884) from the Richmond borehole, Surrey, are described and illustrated, that of J. F. Blake for the first time. The H. H. Winwood Collection is identified as syntypic material of the T. R. Jones & C. D. Sherborn Collection, published in 1888. Sixty-three ostracod species are described of which six are new, and six are left under open nomenclature. Nineteen species are listed as lost. Two genera, *Hadrocytheridea* and *Hekistocythere*, are new.

I. INTRODUCTION

In 1884 T. R. Jones described the foraminifera and Ostracoda from a deep boring at Richmond, Surrey. The ostracods were described from three levels and, apart from *Pontocyprella harrisiana* and *Schuleridea jonesiana* which are Cretaceous contaminants of the collection, are Bathonian in age.

Four years later, Jones & Sherborn (1888) described a much larger ostracod fauna from the Bathonian of Midford, near Bath. The samples of Blue and Yellow Fuller's Earth Clay were given to Jones and Sherborn by the Rev. H. H. Winwood (see Jones & Sherborn 1886).

The collections of Jones 1884, and of Jones & Sherborn 1888, are of considerable importance for present-day work. Because of this it is proposed here to re-describe and re-illustrate the species and to designate types where necessary; a few species originally described by Jones & Sherborn are missing from the collections and are presumed lost.

Two additional collections from the Fuller's Earth of Midford, near Bath, are included because they add to the faunal list and in the case of the Blake collection record the presence, for the first time in England, of a number of species previously only described from N.W. France (Oertli 1959). The most important of the collections, however, is that presented by the Rev. H. H. Winwood. A label stating that these specimens are duplicates of the originals figured in 1888 was left with the collection by C. D. Sherborn. As the specimens figured by Jones & Sherborn were extracted from material given them by Winwood, there would appear to be no doubt that this collection represents syntypic material.

The Fuller's Earth Clay of Midford, near Bath, was placed by Arkell (1956 : 28) in the *Oppelia aspidoides* Zone. Torrens (1967 : 83), however, assigned it to the zone of *Prohecticoceras retrocostatum*, basal Upper Bathonian and below the *aspidoides* Zone.

The terminology and classification employed throughout this paper are those of Moore (1961) and Bate (1963). All the material described is in the Department of Palaeontology, British Museum (Natural History).

II. THE T. R. JONES COLLECTION

Order PODOCOPIDA Müller 1894

Suborder PLATYCOPINA Sars 1866

Family **CYTHERELLIDAE** Sars 1866

Genus ***CYTHERELLA*** Jones 1849

Cytherella symmetrica Jones

(Pl. 1, figs. 1, 2)

1884 *Cytherella symmetrica* Jones : 768, pl. 34, fig. 42.
1884 *Cytherella subovata* Jones : 773, pl. 34, fig. 43.

DIAGNOSIS. *Cytherella* with elongate-oval carapace. Left valve uniformly overreached by larger right valve. Greatest height of carapace in posterior third. Shell surface very finely punctate. Dimorphic: Adult female of length 0·85 mm., male of length 0·90 mm.

LECTOTYPE. IN.43503, female right valve; Richmond boring, depth 1,151 ft. 6 ins.

PARALECTOTYPES. IN.43496, male left valve, and I.941, female carapace; depth 1,205 ft.

DESCRIPTION. Both left and right valves are elongate-oval in outline with well-rounded anterior and posterior margins. Ventral margin straight to slightly convex, dorsal margin strongly convex in the posterior third (region of greatest height) but straightens out anteriorly. Greatest length through mid-point. Right valve larger than the left which it overreaches evenly all-round. Shell surface very finely punctate, though the state of preservation does not always show this. Selvage in the left valve strongly developed to form a ridge which fits into a corresponding groove in the right.

DIMENSIONS. IN.43503. Female right valve and lectotype of *Cytherella symmetrica* Jones, length 0·85 mm.; height 0·52 mm. IN.43496. Male left valve and lectotype of *Cytherella subovata* Jones, length 0·90 mm.; height 0·50 mm. I.941. Female carapace, length 0·77 mm.; height 0·49 mm.; width 0·36 mm.

Remarks. The figured specimens of *C. symmetrica* and of *C. subovata* are missing from the Jones Collection and are presumed lost. Unfigured syntypes have therefore been selected as lectotypes. *C. subovata* has been recognized as the male dimorph and *C. symmetrica* as the female dimorph of the species *Cytherella symmetrica*.

Oval species of *Cytherella* look very much alike, and *C. symmetrica* is very similar to *C. suprajurassica* Oertli (1957 : 649, pl. 1, figs. 1–10). The latter, however, is a smaller species with a greater mid-dorsal projection of the right valve over the left. In *C. symmetrica* the overreach of the right valve is much more uniformly developed along the entire dorsal margin.

Genus ***CYTHERELLOIDEA*** Alexander 1929

Cytherelloidea jugosa (Jones)

(Pl. 1, figs. 3, 4; Text-fig. 1)

1884 *Cytherella jugosa* Jones : 773, pl. 34, fig. 44.

Diagnosis. Carapace sub-rectangular in outline with broadly rounded anterior and posterior margins. Ventral margin strongly incurved. Ornamentation consists of a broad peripheral ridge and a thick, central sigmoid ridge. Shell surface finely punctate.

Lectotype. IN.43497, female right valve (figured Jones 1884); Richmond boring, 1,205 ft.

Paralectotype. I.2311, female carapace; Richmond boring, depth not recorded.

Description. Carapace sub-rectangular in outline with well rounded anterior and posterior margins. Dorsal margin broadly convex with a slight concavity just anterior of mid-point. Ventral margin strongly incurved. Greatest length through mid-point; greatest height median, despite the strong concavity of the ventral margin. Greatest width at the posterior margin. The two specimens available are female dimorphs possessing two posterior swellings, of which the lowermost is the more prominent. Shell surface finely punctate, further ornamented by a broad peripheral ridge extending completely around each valve and enclosing a sigmoid inner ridge which commences at the anterior inner edge of the peripheral ridge, bends upwards, then curves down below the mid-dorsal muscle scar depression, finally curving upwards again to die out before reaching the peripheral ridge in the region ol the postero-dorsal angle. Right valve larger than the left, which it overreaches anteriorly and overlaps ventrally and dorsally, especially anterodorsally where there is a slight concavity in the margin. Only internal details of the right valve observed: **Muscle scars** situated on a slightly raised dorso-median boss, are typical of the genus; a groove extends around the posterior and along the dorsal margin for the reception of the left valve. Two posterior cavities correspond to the swellings seen on the outside of the valve.

DIMENSIONS.

IN.43497. Female right valve, length 0·55 mm.; height 0·30 mm.
I.2311. Female carapace, length 0·56 mm.; height 0·34 mm.; width 0·23 mm.

REMARKS. *C. jugosa* is similar to *C. paraweberi* Oertli (1957 : 651, pl. 1, figs. 12–15) but differs in being rounded rather than angular postero-dorsally, in being more noticeably constricted mid-dorsally, and in being narrower anteriorly where only the right valve tends to project. Laterally, the ribbing of *C. jugosa* is very much broader. A weak reticulation may be observed in *C. paraweberi* on the lateral surface.

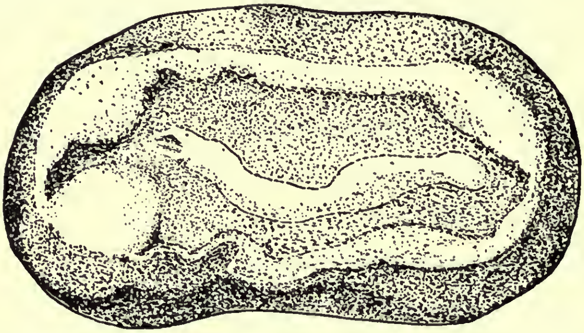


FIG. 1. *Cytherelloidea jugosa* (Jones). Female right valve. Lectotype IN.43497. × 135.

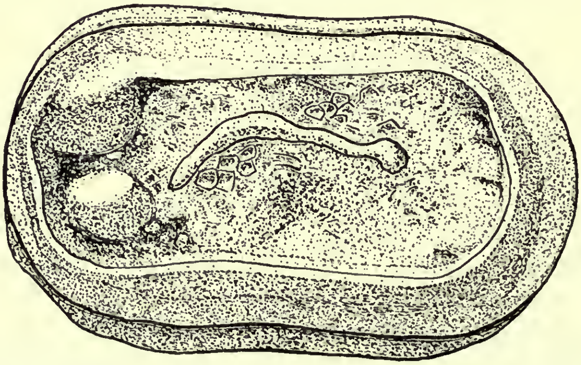


FIG. 2. *Cytherelloidea paraweberi* Oertli. Right side, female carapace, Io.3527. × 130.

Stratigraphically, *C. jugosa* predates *C. weberi* Steghaus (1951 : 207, pl. 14, figs. 3–6) and *C. paraweberi* Oertli, both of which appear to be restricted to the Kimmeridgian. The close similarity in ornamentation between these species suggests a phylogenetic relationship (Text-figs. 1, 2). This is probably also true for the Bajocian species., *Cytherelloidea eastfieldensis* Bate (1963*a* : 25, pl. 1, figs. 1–5, Text-fig. 1) which is easily distinguishable by the mid-dorsal discontinuity of the peripheral ridge.

Suborder PODOCOPINA Sars 1866

Superfamily **BAIRDIACEA** Sars 1888

Family **BAIRDIIDAE** Sars 1888

Genus ***BAIRDIA*** McCoy 1844

Bairdia hilda Jones

(Pl. 1, figs. 5, 6; Pl. 4, fig. 5)

1884 *Bairdia hilda* Jones : 771, pl. 34, fig. 20.
1888 *Bairdia fullonica* Jones & Sherborn : 253, pl. 5, fig. 4*a–c*.
1948 *Bairdia* cf. *hilda* Jones; Sylvester-Bradley : 199, Text-fig. 5.
1963 *Bairdia hilda* Jones; Bate : 188, pl. 2, figs. 9–12, pl. 3, figs. 1–4.
1964 *Bairdia hilda* Jones; Bate : 8.

Diagnosis. Carapace subdeltoid laterally, strongly convex dorsally. Dorsal margin high with steeply inclined anterior and posterior slopes. Posterior end acuminate, upturned. Shell surface finely punctate.

Lectotype. IN.41951, single left valve figured Jones (1884) Richmond boring, depth 1,205 ft.

Paralectotypes. Io.3608–16 and Io.3620–6, carapaces and single valves from a depth of 1,205 ft.

Remarks. Full descriptions of this species have been given previously by Sylvester-Bradley (1948) and Bate (1963). However, as the measurements of the types were not included these are given here.

Dimensions. IN.41951, left valve, length 0·93 mm.; height 0·48 mm. Io.3608. carapace, length 0·77 mm.; height 0·48 mm.; width 0·34 mm. Io.3610, carapace, length 0·90 mm.; height 0·47 mm.; width 0·34 mm.

Bairdia juddiana Jones

(Pl. 1, fig. 7)

1884 *Bairdia juddiana* Jones : 767, pl. 34, fig. 18.

Diagnosis. Carapace globose, convex in dorsal view. Shell surface finely punctate. Antero-dorsal and postero-dorsal slopes convex. Left valve distinctly overlaps the right along the dorsal and ventral margins, particularly mid-ventrally. Caudal process slightly upturned. Ventral margin angled with flattened median portion and steeply sloping antero-ventral and postero-ventral slopes.

Holotype. IN.43506, carapace, figured Jones (1884), Richmond boring, depth 1,151 ft.–1,151 ft. 6 in.

Description. Carapace rather globose in lateral view with convex antero-dorsal and postero-dorsal slopes. Anterior end rounded, posterior end with caudal process slightly upturned although damaged in the specimen available. Dorsal margin with convex central section and steeply sloping antero-dorsal and postero-dorsal slopes. Greatest length of carapace through the mid-point; greatest height and width slightly anterior to the mid-point. Left valve larger than the right which it overlaps along the entire dorsal and ventral margins and overreaches slightly at the anterior margin. Shell surface finely punctate. Internal features not known.

Dimensions. IN.43506, carapace, length 0·85 mm.; height 0·59 mm.; width 0·46 mm.

Remarks. *Bairdia juddiana* is sufficiently distinct for the single carapace to be considered a separate species; it differs from *B. hilda* in being shorter, higher and more strongly convex in dorsal view. The postero-dorsal slope of *B. hilda* is more strongly concave than that of *B. juddiana* which lacks the slight anterior upturning of the antero-dorsal slope seen in the former.

Bairdia jurassica Jones

(Pl. 2, figs. 1, 2)

1884 *Bairdia jurassica* Jones : 771, pl. 34, fig. 21.
1884 *Bairdia jurassica* var *tenuis* Jones : 771, pl. 34, fig. 22.

Diagnosis. Carapace elongate, drawn out, with acuminate slightly upturned caudal process. Dorsal margin broadly arched with obliquely sloping antero-dorsal and postero-dorsal slopes. Left valve larger than the right which it overlaps antero-dorsally, postero-dorsally and mid-ventrally. Postero-ventrally, the left valve turned outwards to reveal margin of right valve. Shell surface very finely punctate.

Lectotype. IN.43494, figured Jones 1884, pl. 34, fig. 21, Richmond boring, depth 1,205 ft.

Paralectotypes. IN.43495, figured Jones 1884, pl. 34, fig. 22, and Io.3617, carapaces from depth 1,205 ft., Richmond boring.

Description. Carapace drawn out, elongate, greatest length just below mid-point. Greatest height and width just anterior to mid-point. Dorsal margin broadly arched with the antero- and postero-dorsal slopes obliquely inclined and only slightly convex. Anterior end rounded, posterior end acuminate, not prominently upturned. Ventral margin broadly convex, almost straight. Left valve larger than the right which it overlaps along the antero-dorsal and postero-dorsal slopes, especially towards the extreme anterior, and posteriorly along the caudal process. Left valve overlap prominent mid-ventrally; left valve very noticeably turned outwards postero-ventrally from the right to reveal the margin of the right valve. Shell surface finely punctate. Internal features not seen.

Dimensions. IN.43494, carapace, length 0·85 mm.; height 0·39 mm.; width 0·31 mm. IN. 43495, carapace, length 0·93 mm.; height 0·40 mm.; width 0·34 mm. Io.3617, carapace, length 0·88 mm.; height 0·43 mm.; width 0·30 mm.

Remarks. From the dimensions given above it can be seen that the variety *tenuis* is more elongate than the other two specimens. Some variants of *Bairdia hilda* Jones are similar to the present species which may be distinguished on the shape of its carapace and the type of overlap by the left valve.

Superfamily **CYPRIDACEA** Baird 1845

Family **PARACYPRIDIDAE** Sars 1923

Genus ***PONTOCYPRELLA*** Ljubimova 1955

Pontocyprella harrisiana (Jones 1849)

(Pl. 2, fig. 3)

1849 *Bairdia harrisiana* Jones : 25, pl. 6, figs. 17*a–f*.
1884 *Macrocypris bradiana* Jones : 766, pl. 34, fig. 23.

For a full synonymy of Cretaceous forms see Kaye 1965 : 73.

Material. IN.43500, left valve figured Jones (1884), depth 1,145 ft. 9 in.–1,146 ft. 6 in.

Remarks. Jones (1849 : 25) first recorded this species as *Bairdia harrisiana* from a number of horizons, but typically from the Cretaceous (Gault, Leacon Hill; Chalk, Gravesend and Charlton; Detritus, Charing and from the Speeton Clay, Yorkshire).

The presence of this species at a depth of 1,145 ft. 9 in.–1,146 ft. 6 in. in the Richmond bore indicates that some contamination of the cored material has occurred. As Jones himself originally described *P. harrisiana*, it is somewhat surprising that he failed to recognize it here.

Dimensions. IN.43500, left valve, length 0·88 mm.; height 0·42 mm.

Superfamily **CYTHERACEA** Baird 1850

Family **SCHULERIDEIDAE** Mandelstam 1959

Subfamily **SCHULERIDEINAE** Mandelstam 1959

Genus ***SCHULERIDEA*** Swartz & Swain 1946

Schuleridea (Schuleridea) jonesiana (Bosquet)

(P.l 2, fig. 5)

1884 *Cytheridea subperforata* Jones : 772, pl. 34, fig. 26, [not p. 768, pl. 34, fig. 25].

For the synonymy of the Cretaceous forms see Kaye 1964 : 45.

Material. IN.43490, carapace, figured Jones (1884), Richmond boring, 1,205 ft.

Remarks. The specimen described by Jones (1884 : 768) from 1,151 ft.–1,151 ft. 6 in. in the Richmond boring is not conspecific with that described from 1,205 ft. The latter is a Cretaceous contaminant.

Dimensions. IN.43490, carapace, length 0·95 mm.; height 0·60 mm.; width 0·43 mm.

Schuleridea* (*Eoschuleridea*) *subperforata (Jones)

(Pl. 2, fig. 4)

1884 *Cytheridea subperforata* Jones : 768, pl. 34, fig. 25, [not p. 772, pl. 34, fig. 26].

LECTOTYPE. IN.43504, right valve, figured Jones 1884, pl. 34, fig. 25. Richmond boring, 1,151 ft.- 1,151 ft. 6 in.

REMARKS. Male right valve elongate-oval in outline with a characteristic prominence in the region of the anterior cardinal angle. Antero-dorsal slope short, steeply inclined, and concave. Anterior and posterior ends rounded; ventral margin convex with a prominent antero-ventral incurvature. At least twenty-one anterior radial pore canals in typical fan-like arrangement. Hinge broken, terminal teeth incomplete. Duplicature well developed, particularly postero-ventrally. Poor preservation prevents further description.

In outline this species is similar to the male dimorph of *Schuleridea* (*Eoschuleridea*) *bathonica* Bate (1967 : 41) but may be distinguished by the antero-dorsal prominence in the region of the cardinal angle and being slightly more narrowly rounded posteriorly.

DIMENSIONS. IN.43504, right valve, length 0·73 mm.; height 0·39 mm.

Schuleridea* (*Eoschuleridea*) *trigonalis (Jones)

(Pl. 2, fig. 7)

1884 *Bairdia trigonalis* Jones : 767, pl. 34, fig. 19.

DIAGNOSIS. Carapace trigonal in outline with high dorsal margin: Dorsum short, slightly convex, posteriorly sloping in right valve; umbonate left valve which prominently overreaches the right. Greatest length of carapace below mid-point. Greatest height anterior of mid-point in right valve, through mid-point in left. Anterior end rounded, posterior strongly acuminate. Antero- and postero-dorsal slopes steeply inclined. Anterior radial pore canals few in number.

HOLOTYPE. IN.42373, carapace figured Jones 1884, pl. 34, fig. 19; Richmond boring, depth 1,151 ft.–1,151 ft. 6 in.

DESCRIPTION. Carapace strongly trigonal in lateral view with the umbonate left valve projecting noticeably above the right. Posterior end strongly acuminate, anterior end rounded. Greatest length of carapace below mid-point; greatest height of the left valve through mid-point and of the right valve slightly forward of this. Greatest width median. Ventral margin broadly convex; dorsal margin in the right valve short and slightly convex, sloping to the posterior. Dorsal margin in the left valve strongly umbonate. Antero-dorsal and postero-dorsal slopes steeply inclined, slightly convex. Shell surface very finely punctate. Left valve larger than the right which it overlaps along the ventral margin, around the posterior and along the antero-dorsal and postero-dorsal slopes. Mid-dorsally the left valve projects strongly above the right. Internal details not seen. Anterior radial pore canals not clearly seen but appear to be relatively few.

DIMENSIONS. IN.42373, carapace, length 0·70 mm.; height 0·48 mm.; width 0·36 mm.

REMARKS. If the species is dimorphic, the holotype must be that of a female carapace. A species close to this is *Schuleridea* (*Eoschuleridea*) *bathonica* Bate (1967 : 41) from which it may be distinguished by the strongly umbonate left valve and the more strongly acuminate posterior.

Genus ***PRAESCHULERIDEA*** Bate 1963

Praeschuleridea schwageriana (Jones)

(Pl. 2, fig. 6)

1884 *Cythere schwageriana* Jones : 766, pl. 34, fig. 27.

DIAGNOSIS. Carapace oval in outline with the left valve projecting above the right. Postero-dorsal slope of left valve rounded, posterior rounded. Shell surface finely punctate.

HOLOTYPE. IN.43499, female carapace, figured Jones 1884, pl. 34, fig. 27. From depth 1,145 ft. 9 in.–1,146 ft. 6 in.

DESCRIPTION. Carapace oval in outline with rounded anterior and posterior margins. Ventral margin broadly, but not strongly convex in left valve, somewhat flattened in the right valve. Dorsal margin strongly convex in the left valve, projecting above the right. Anterior cardinal angle rounded, posterior angle more sharply acute. Postero-dorsal slope steeply inclined, more strongly convex in the left valve. Antero-dorsal slope convex in both valves. Greatest length through mid-point. Greatest height median; greatest width slightly behind mid-point. Shell surface finely punctate. Left valve larger than the right. No internal features observed.

DIMENSIONS. IN.43499, female carapace, length 0·60 mm.; height 0·39 mm.; width 0·31 mm.

REMARKS. Jones (1884) referred to but a single specimen for this species and illustrated a left valve. However, in the plate description he referred to fig. 27 as a right valve. The actual specimen is in fact a complete carapace, and in the absence of any evidence to the contrary is considered here to be the holotype.

Praeschuleridea schwageriana is similar to *P. subtrigona* (Jones & Sherborn 1888) but is larger and less angular posteriorly: it is close to *P. subtrigona intermedia* Bate (1965) but may be distinguished by the more uniformly rounded posterior end. Given more material showing only slight variation in outline, it might not be possible to distinguish *P. schwageriana* from one of the subspecies of *P. subtrigona*.

Praeschuleridea sp.

(Pl. 2, fig. 8)

Description. Carapace trigonal in outline with the left valve strongly umbonate and projecting above the right valve. Strongly convex when viewed dorsally. Greatest length, height (left valve) and width pass through mid-point. Right valve somewhat umbonate in the region of the anterior cardinal angle, below which there is a deep, oblique groove. Left valve larger than the right. Anterior and posterior margins rounded; ventral margin broadly convex. Internal details not seen. Anterior radial pore canals in part seen from the exterior and appear typical for the genus.

Dimensions. Io.3619, female carapace, length 0·59 mm.; height 0·43 mm.; width 0·35 mm.

Remarks. This somewhat globose, triangular ostracod is similar in general outline to *Schuleridea trigonalis* (Jones 1884), but differs most markedly in that the line of greatest length passes through mid-point and not below it as in the latter species.

This species of *Praeschuleridea* is almost certainly new and was found in a slide of duplicate material obtained from the Richmond boring; depth 1,151 ft. 6 in. It is considered inadvisable to erect a new species on only a single specimen.

Family **PROGONOCYTHERIDAE** Sylvester-Bradley 1948

Subfamily **PROGONOCYTHERINAE** Sylvester-Bradley 1948

Genus ***GLYPTOCYTHERE*** Brand & Malz 1962

Glyptocythere guembeliana (Jones)

(Pl. 3, figs. 1, 2; Pl. 4, fig. 1)

1884 *Cythere guembeliana* Jones : 772, pl. 34, figs. 32, 33, [not fig. 31].
1888 *Cytheridea pulvinar* Jones & Sherborn : 266, pl. 3, figs. 2*a–c*.
1888 *Cytheridea trapezoidalis* Terquem, Jones & Sherborn : 270, pl. 4, figs. 1*a*, *b*.
1967 *Glyptocythere guembeliana* (Jones) Bate : 49, pl. 13, figs. 10–16, pl. 14, figs. 1–8.

Diagnosis. Carapace subquadrate, elongate in male dimorph. Lateral surface with transverse ridges extending down from dorsal margin, though generally poorly developed. Marginal borders compressed. Ventro-lateral margin evenly convex in female, sharply directed upwards posteriorly in male right valve. Hinge weakly entomodont.

Lectotype. IN.43493, male right valve from Richmond boring, depth 1,205 ft. Figured Jones (1884, pl. 34, fig. 33).

Paralectotype. Io.3338, male carapace from same depth.

Remarks. This species was revised by Bate (1967 : 49). The specimen illustrated is the lectotype (IN.43493) figured by Jones 1884, pl. 34, fig. 33, and recorded from a depth of 1,205 ft. The specimen for fig. 32 is missing and that of fig. 31 is not considered conspecific.

Dimensions. Lectotype: IN.43493, male right valve, length 0·96 mm.; height 0·49 mm.

Genus *FASTIGATOCYTHERE* Wienholz 1967

Fastigatocythere juglandica (Jones)

(Pl. 3, figs. 4, 7, 8; Pl. 12, fig. 3)

1884 *Cythere juglandica* Jones : 766, 768, pl. 34, figs. 36, 37.
1888 *Cythere juglandica* var. major Jones & Sherborn : 225, pl. 4, figs. 2*a*–*b*.
1948 *Progonocythere juglandica* (Jones) Sylvester-Bradley : 193, pl. 12, figs. 5, 6, pl. 13, fig. 8.
1963 *Progonocythere juglandica juglandica* (Jones); Grekoff : 1731, pl. 3, fig. 55.
1963 *Progonocythere? juglandica* (Jones); Oertli : pls. 28, 29, 30.
1967 *Glyptocythere juglandica* (Jones) Bate : 51.

Diagnosis. Carapace sub-rectangular tapering strongly to posterior end. Left valve larger than right, projecting above right valve dorsally, except mid-dorsally where the umbonate right valve strongly projects. Ornamentation of transverse ridges and reticulae radiate down from dorsal margin. Ventro-lateral margins convex; carapace swollen medially. Flattened marginal borders. Hinge entomodont.

Lectotype. IN.41947, right valve. Richmond boring, 1,146 ft. Figured Jones (1884).

Paralectotypes. IN.41948–9. Two carapaces from 1,151 ft. 6 in.

Remarks. This species was described by Sylvester-Bradley (1948) who placed it in his new genus *Progonocythere*. Brand & Malz (1962) removed from that genus those species which have a more quadrate outline, which possess a distinct ornamentation not usually present in species of *Progonocythere* s.s., and which also have a dorsal projection of the dorso-median part of the right valve. The last feature was noted by Sylvester-Bradley (1948 : 194) and used by Bate (1967 : 51) to justify the assignment of this species to *Glyptocythere*. Subsequently Wienholz (1967 : 25) separated from *Glyptocythere* those species which have a more elongate carapace outline, a more positive antero-dorsal furrow and strongly diverging ribs radiating from the dorsal margin. For these species Wienholz erected the genus *Fastigatocythere*, to which she assigned *juglandica*. This assignment is accepted here.

Dimensions. Lectotype: IN.41947, right valve, length 0·93 mm.; height 0·47 mm. IN.41948, carapace, length 0·87 mm.; height 0·51 mm.; width 0·49 mm. IN.41949, carapace, length 0·77 mm.; height 0·49 mm.; width 0·49 mm.

Genus *LOPHOCYTHERE* Sylvester-Bradley 1948

Remarks. There is an understandable reluctance on the part of some ostracod workers to identify a genus or subgenus simply on an ornamental variation. However, some ostracod lineages fall naturally into morphological groups in which a particular ornamental trend is evident. I feel that within the Ostracoda there is ornamentation of a primary kind which reflects a generic or possibly subgeneric status, and a secondary ornamentation of a more specific character. The latter might be superimposed upon the former or simply modify it.

Lophocythere clearly contains two distinct morphological groups: the first centred around *Lophocythere ostreata* (Jones & Sherborn 1888) with an L-shaped ridge extending around the anterior margin and bending back along the ventro-lateral margin as the diagnostic character, and the second around *L. bradiana* (Jones 1884), in which several ridges extend across the lateral surface of the carapace.

Whatley (personal communication) informs me that he has, in manuscript, subdivided the genus *Lophocythere* accordingly. As this information will shortly be published by him it is not my intention to deal further with this generic revision.

Lophocythere bradiana (Jones)

(Pl. 3, figs. 3, 5, 6; Text-figs. 3, 4)

1884 *Cythere bradiana* Jones : 772, pl. 34, figs. 38*a–b*.
1888 *Cytheridea craticula* Jones & Sherborn : 272, pl. 4, figs. 9*a–c*, 10*a–c*.
1948 *Lophocythere bradiana* (Jones) Sylvester-Bradley : 196, pl. 14, figs. 7–10, pl. 15, figs. 8–11.

DIAGNOSIS. Carapace subrectangular, dimorphic. Left valve larger than, and projects dorsally above, the right. Anterior end broadly rounded, posterior end triangular with greatest length of carapace through mid-point. Cardinal angles prominent, rounded. Eye swelling situated at anterior cardinal angle. Lateral surface ornamented by four major carinae: dorsal carina originates at, or a short distance from, the anterior margin, curves under the eye swelling, to which a short offshoot runs, then curves back over dorso-median part of valve to die out below posterior cardinal angle. The second carina originates at the antero-ventral margin, runs parallel to the dorsal carina for a short distance then bifurcates, the two branches running parallel almost to the posterior end where they converge and almost meet. The fourth carina originates at the antero-ventral margin then follows a course roughly parallel to lowermost of the two median carinae. A short carina occurs between the ventral carina and the lowest median carina in the anterior half of the valve. A second short carina, convex dorsally, occurs between the dorsal carina and the uppermost of the two median carinae in the posterior half of the valve, in which region a short, straight carina, is sometimes developed between the two median carinae. Shell surface reticulate between the carinae.

LECTOTYPE. IN.42372, male carapace, figured Jones (1884), Richmond boring, depth 1,205 ft.

PARALECTOTYPES. Io.3627–9, one male and two female carapaces from depth 1,205 ft.

DESCRIPTION. Carapace subrectangular, more elongate in the male dimorphs. Dorsal and ventral margins virtually parallel, with rounded anterior, and triangular posterior margins. Cardinal angles prominent, rounded, especially prominent in the larger left valve, the dorsal margin of which projects above the right. Ventral surface ornamented with three longitudinal ridges per valve. Left valve uniformly overlaps the right along the ventral margin, more strongly so antero-ventrally. Greatest length of carapace through mid-point, greatest height in the anterior third, greatest width in the posterior third. Ornamentation of lateral surface as in the diagnosis. **Eye swelling** prominently situated below the anterior cardinal angle. Details of hinge not known from the type material although it is entomodont in comparative material.

DIMENSIONS. IN.42372, male carapace, length 0·61 mm.; height 0·32 mm.; width 0·29 mm. Io.3627, male carapace, length 0·65 mm.; height 0·34 mm.; width 0·30 mm. Io.3628, female carapace, length 0·57 mm. height 0·34 mm.; width 0·29 mm. Io.3629, female carapace, length 0·66 mm.; height 0·39 mm.; width 0·34 mm.

REMARKS. Sylvester-Bradley (1948) placed *Cytheridea bradiana* Jones & Sherborn in synonymy with *Cythere bradiana* Jones. However, the specimen described by Jones & Sherborn is not conspecific but is a paralectotype of *Lophocythere septicostata* Bate (1967 : 52, pl. 15, figs. 7–13, pl. 16, figs. 1–4).

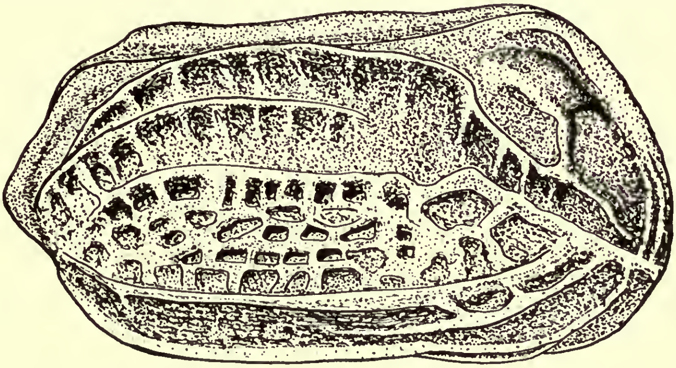


FIG. 3. *Lophocythere bradiana* (Jones). Right valve, complete carapace of lectotype of *Cytheridea bradiana* Jones. IN.42372. × 140.

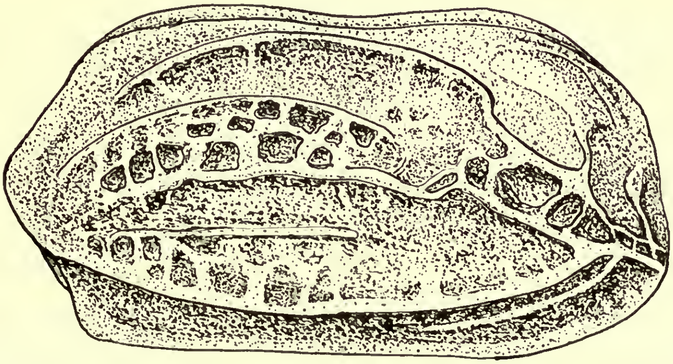


FIG. 4. *Lophocythere bradiana* (Jones). Right valve, complete carapace of lectotype of *Cytheridea craticula* Jones & Sherborn. I.1854. × 140.

Sylvester-Bradley (1948 : 197) considered *Cytheridea craticula* Jones & Sherborn 1888 to be a subspecies of *bradiana* because " there is a short anterior stem from which spring the dorsal, the two median, and the ventral carinae ". Examination of the types of *bradiana* and of *craticula* show this is not, in fact so. The dorsal carina does not in all specimens reach the anterior margin. Where the reticulate ornamentation is particularly well developed a cross reticulation gives the impression that the dorsal carina is joined to the median carina. The ventral carina originates at the antero-ventral margin, and it is the short carina situated between this and the lowermost median carina which sometimes joins the stem of the two median carinae.

Although the lectotype of *L. bradiana* shows the development of a low ridge or carina between the two median carinae in the posterior part of the valve, many specimens do not show this feature. It is, however, well developed in the male paralectotype, Io.3627, and should not be regarded as being a feature of *craticula* even though the lectotype of the latter shows it remarkably well.

To summarize, the variations found within a population of *Lophocythere bradiana*, such as the occasional imperfect development of the dorsal carina close to the anterior margin and the presence or absence of a short carina posteriorly between the two median carinae, do not indicate either a separate species or subspecies, but are part of the normal variation present in the species.

L. bradiana is followed in the Oxfordian of France by *L. multicostata* Oertli (1957), a species which has a similar ornamentation. However, *L. multicostata* does not possess the anterior carina situated between the ventral and lower median carina of *bradiana*, but has an additional anterior ridge in front of the eye swelling.

The variations within *Lophocythere bradiana* are illustrated in Text-figs. 3, 4.

Genus ***MICROPNEUMATOCYTHERE*** Bate 1963

Micropneumatocythere subconcentrica (Jones)

(Pl. 4, fig. 7)

1884 *Cythere subconcentrica* Jones : 768, pl. 34, figs. 28, 29.
1967 *Micropneumatocythere subconcentrica* (Jones) Bate : 60, pl. 21, figs. 1–13.

DIAGNOSIS. *Micropneumatocythere* with oval carapace tapering posteriorly. Ventro-lateral margin swollen. Shell surface punctate laterally. Ventral surface with longitudinal ridges extending on to ventro-lateral margin and turning upwards anteriorly and posteriorly. Internal details as for genus.

LECTOTYPE. IN.43505, left valve from Richmond boring, depth 1,151 ft. 6 in. Figured Jones (1884, pl. 34, fig. 28).

REMARKS. This species has been revised by Bate (1967 : 60) and need not be dealt with fully here. The lectotype, a left valve, is considered to be the specimen figured by Jones although the caption to the figure states that it is a right valve.

DIMENSIONS. IN.43505, left valve, length 0·56 mm.; height 0·38 mm.

Genus *TERQUEMULA* Blaszyk & Malz 1965

Terquemula blakeana (Jones)

(Pl. 4, fig. 8; Pl. 5, fig. 1)

1884 *Cythere blakeana* Jones : 772, pl. 34, figs. 34, 35.
1888 *Cytheridea transversiplicata* Jones & Sherborn : 267, pl. 3, fig. 4.
?1888 *Cytheridea blakeana* (Jones), Jones & Sherborn : 265, pl. 2, fig. 11.
1888 *Cytheridea egregia* Jones & Sherborn : 267, pl. 3, fig. 5.
1948 *Progonocythere blakeana* (Jones), Sylvester-Bradley : 191, pl. 12, figs. 3, 4, pl. 13, figs. 4, 5.
1959 *Progonocythere ? blakeana* (Jones), Triebel & Klingler : 339, 341.
1963 *Progonocythere ? blakeana* (Jones), Oertli : 36, pl. 25, fig. *c*, pl. 26, fig. *c*, pl. 27, fig. *c*, pl. 28, fig. *c*, pl. 30, fig. *c*.
1965 *Terquemula blakeana* (Jones), Blaszyk & Malz : 445.

DIAGNOSIS. Carapace oval-elongate, noticeably constricted mid-dorsally and mid-ventrally. Anterior end rounded, posterior end narrowly rounded. Postero-lateral part of carapace swollen, overreaching ventral margin. Greatest length through or slightly above mid-point. Shell surface with large, sunken normal pore canal openings and a broad reticulation of wrinkles. Muscle scars of Type **A** (Bate 1963 : 180). Species dimorphic. Hinge entomodont.

LECTOTYPE. IN.41950, female left valve, Richmond boring, depth 1,205 ft. Figured Jones (1884).

REMARKS. This species was described fully by Sylvester-Bradley (1948). The type specimen of *Cytheridea egregia* Jones & Sherborn, placed by Sylvester-Bradley in synonymy with *blakeana*, has been lost, but the original illustration (pl. 3, fig. 5) suggests that the synonymy is justified.

The specimen described as *C. blakeana* by Jones & Sherborn could be a juvenile form of another specimen as suggested by Sylvester-Bradley (1948 : 193).

DIMENSIONS. Lectotype: female left valve, length 0·69 mm.; height 0·39 mm.

Family **CYTHERURIDAE** Müller 1894

Genus *METACYTHEROPTERON* Oertli 1957

Metacytheropteron drupaceum (Jones)

(Pl. 5, figs. 4–6)

1884 *Cythere drupacea* Jones : 772, pl. 34, fig. 30.
1957*a* *Metacytheropteron* sp. 50, Oertli : table 1.
1963 *Cytheropteron jonesanum* Coryell : 854.
1967 *Metacytheropteron drupacea* (Jones); Bate : 44, pl. 10, figs. 1–9.

DIAGNOSIS. *Metacytheropteron* with elongate/sub-ovate carapace. Greatest height at anterior cardinal angle, posterior end acuminate. Dorsal margin broadly convex, especially in left valve. Shell surface strongly ornamented with triangular arrangement of longitudinal and obliquely transverse ridges.

Holotype. IN.43498, female carapace from Richmond boring, depth 1,205 ft. Figured Jones (1884).

Remarks. Coryell (1963) renamed this species *Cytheropteron jonesanum* on the assumption that *C. drupacea* mentioned by Richter (1867 : 228) and *Cythere drupacea* of Jones were homonyms. Reference to Richter (1855 : 529), however, indicates that the species referred to in 1867 had been placed in *Cythereis* and not *Cythere* as supposed by Coryell. There is, therefore, no nomenclatural problem.

Dimensions. Holotype. IN.43498, carapace, length 0·50 mm.; height 0·30 mm.; width 0·29 mm.

Family **TRACHYLEBERIDIDAE** Sylvester-Bradley 1948

Genus ***CYTHEREIS*** Jones 1849

Cythereis cf. ***blanda*** Kaye 1963

(Pl. 5, figs. 3, 7)

1884 *Cythere* (*Cythereis*) *quadrilatera* (Roemer), Jones : 766, 772, pl. 34, figs. 39, 40, 41.

Remarks. Jones recorded *Cythereis quadrilatera* Roemer from two horizons in the Richmond boring (1,145 ft. 9 in.–1,146 ft. 6 in., and 1,205 ft.). These specimens are probably conspecific with *Cythereis blanda* Kaye (1963), although the median and ventro-lateral ridges in Jones's material tend to be more straight and less strongly developed than in *C. blanda*. But this may be within the species' variation.

Jones referred to three specimens, here regarded as Cretaceous contaminants, of *Cythere* (*Cythereis*) *quadrilatera* but only two now remain; these are a complete carapace, IN.43491, figured Jones 1884, pl. 34, fig. 40, and a single left valve IN.43502, figured pl. 34, fig. 39. The specimen illustrated by fig. 41 is missing and the illustration suggests that this latter specimen was not conspecific with the other two.

Dimensions. IN.43491, carapace, length 0·77 mm.; height 0·46 mm.; width 0·32 mm. IN.43502, left valve, length 0·66 mm.; height 0·43 mm.

Family and Genus uncertain

" ***Cythere*** " ***tenella*** Jones

(Pl. 5, fig. 8)

1884 *Cythere tenella* Jones : 772, pl. 34, fig. 24.

Remarks. This small, poorly-preserved ostracod is probably a juvenile instar.

Holotype. IN.43492, complete carapace, Richmond boring, depth 1,205 ft.

Dimensions. Length 0·38 mm.; height 0·21 mm.; width 0·15 mm.

III. THE T. R. JONES & C. D. SHERBORN COLLECTION AND THE H. H. WINWOOD COLLECTION

The following figured specimens of species described by Jones & Sherborn (1888) are no longer represented in their collection and may be presumed lost. Only the first five are known to have been presented to the Museum.

Bairdia juddiana Jones, p. 253.
Cytheridea bicarinata Jones & Sherborn, p. 270, pl. 4, figs. 5*a–c*.
Cytheridea renoides Jones & Sherborn, p. 266, pl. 3, figs. 1*a–c*.
Cytheridea winwoodiana Jones & Sherborn, p. 259, pl. 1, figs. 2*a–d*.
Cytheridea eximia Jones & Sherborn, p. 273, pl. 5, figs. 5*a–c*.
Bairdia trigonalis Jones, p. 253.
Bythocypris winwoodiana Jones & Sherborn, p. 252, pl. 5, figs. 1*a–c*.
Cythere juglandica var. *minor* Jones & Sherborn, p. 255, pl. 4, figs. 3*a–c*.
Cythere ? speciosa Jones & Sherborn, p. 254, pl. 2, figs. 10*a–c*. (This species was recorded as lost by Jones & Sherborn, p. 254.)
Cythere trapezioides Jones & Sherborn, p. 256, pl. 5, figs. 10*a–c*.
Cythere walfordiana Jones & Sherborn, p. 255, pl. 5, figs. 9*a–c*.
Cytheridea egregia Jones & Sherborn, p. 267, pl. 3, figs. 5*a–c*.
Cytheridea politula Jones & Sherborn, p. 265, pl. 5, figs. 7*a–c*.
Cytheridea pura Jones & Sherborn, p. 269, pl. 3, figs. 11*a–d*.
Cytheridea retorrida Jones & Sherborn, p. 260, pl. 1, figs. 8*a–c*.
Cytheridea rugifera Jones & Sherborn, p. 271, pl. 5, figs. 11*a–c*.
Cytheridea sedata Jones & Sherborn, p. 261, p. 1, figs. 10*a–c*.
Cytheridea subeminula Jones & Sherborn, p. 261, pl. 5, figs. 8*a–c*.
Cytheridea ventrosa Jones & Sherborn, p. 269, pl. 3, figs. 10*a–c*.
Cythereis walfordiana Jones & Sherborn, p. 257, pl. 5, figs. 12*a–c*.

Order PODOCOPIDA Müller 1894

Suborder PLATYCOPINA Sars 1866

Family **CYTHERELLIDAE** Sars 1866

Genus ***CYTHERELLA*** Jones 1849

Cytherella fullonica Jones & Sherborn

(Pl. 5, fig. 9; Pl. 6, fig. 1)

1888 *Cytherella fullonica* Jones & Sherborn : 274, pl. 1, figs. 12*a–c*.
1963 *Cytherella fullonica* Jones & Sherborn; Bate : 184, pl. 1, figs. 1, 2.

DIAGNOSIS. Carapace subrectangular with characteristically steep postero-dorsal slope. Shell surface smooth, with dorso-median muscle-scar depression.

LECTOTYPE. I.1857, left valve, figured Jones & Sherborn 1888, from the Blue Fuller's Earth Clay.

PARALECTOTYPES. I.4004 (Jones & Sherborn Collection); Io.3636–41 (Winwood Collection), left and right valves. Three specimens from the Blue, and four from the Yellow Fuller's Earth Clay.

REMARKS. This species has been previously described in Bate (1963 : 184).

DIMENSIONS. Lectotype: I.1857, left valve, length 0·64 mm.; height 0·34 mm. Paralectotype Io. 4004, left valve, length 0·58 mm.; height 0·32 mm.

Genus ***CYTHERELLOIDEA*** Alexander 1929

Cytherelloidea catenulata (Jones & Sherborn)

(Pl. 6, figs. 2, 3)

1888 *Cytherella catenulata* Jones & Sherborn : 274, pl. 5, figs. 6*a–c*.
1948 *? Cytherelloidea catenulata* (Jones & Sherborn) Sylvester-Bradley : 200, pl. 14, fig. 11.
1963 *Cytherelloidea catenulata* (Jones & Sherborn); Bate : 184, pl. 1, figs. 3–6.
1963 *Cytherelloidea catenulata* (Jones & Sherborn); Oertli : 37, pls. 27, 29.
1964 *Cytherelloidea catenulata* (Jones & Sherborn); Bate : 8.

DIAGNOSIS. Carapace with crescent-shaped swelling situated close to posterior margin of valve. Dorsal limb of crescent bends over and curves forwards close to ventral margin to produce a swelling shaped like a question mark. Shell surface ornamented with longitudinal and terminal (parallel to margins) striae producing a reticulation.

LECTOTYPE. I.1876, left valve, figured Jones & Sherborn, from the Blue Fuller's Earth Clay.

PARALECTOTYPES. I.1846 (left valve) and Io.3525 (right valve), Jones & Sherborn Collection; Io.3649–53, left and right valves from the Winwood Collection. All specimens from the Blue Fuller's Earth Clay.

REMARKS. This species was described by Bate (1963 : 184–5).

DIMENSIONS. I.1876, left valve, length 0·68 mm.; height 0·37 mm. I.1846, left valve; length 0·68 mm.; height 0·36 mm. Io.3525, right valve, length 0·68 mm.; height 0·38 mm.

Cytherelloidea refecta (Jones & Sherborn)

(Pl. 6, figs. 4–7)

1888 *Cytheridea refecta* Jones & Sherborn : 262, pl. 2, figs. 3*a*, *b*.

DIAGNOSIS. Carapace oval, more elongate in male dimorph. Anterior and posterior margins rounded. Posterior cardinal angle prominent, postero-dorsal slope slopes steeply to posterior. Central part of valve with broad depression bounded below by broad crescentic swelling. Crescentic furrow delimits lower surface of swelling. A small rounded swelling is situated to the inside of the anterior part of crescentic swelling.

LECTOTYPE. I.1850, female right valve, figured Jones & Sherborn (1888), from the Blue Fuller's Earth Clay.

PARALECTOTYPES. Io.3931–2, female left valve and male left valve from the Winwood Collection. Both specimens from the Blue Fuller's Earth Clay.

DESCRIPTION. Carapace oval in outline with rounded anterior and posterior margins and prominent posterior cardinal angle. The postero-dorsal slope is steeply inclined, but slightly convex. Dorsal margin of both valves slightly concave antero-medially. Ventral margin convex in the right valve, concave in the left. Shell surface with a broad, deep furrow, crescentic in shape which commences postero-dorsally and terminates antero-dorsally. Above this furrow a broad swelling is developed, also crescentic but rather irregular in outline. Anteriorly the swelling appears to turn back sharply upon itself for a short distance before dying out. To the inside of this swelling and situated in the angle of the anterior turn-back, a small circular swelling is developed. The main crescentic swelling is delimited on its dorsal side by a broad central depression. In the region of the anterior margin the surface of the shell may be seen to be weakly reticulate. Internally the dorsal edge of the right valve possesses a groove for the reception of the valve margin of the smaller left valve.

DIMENSIONS. I.1850, female right valve, length 0·60 mm.; height 0·26 mm. Io.3931, female left valve, length 0·52 mm.; height 0·28 mm. Io.3932, male left valve, length 0·71 mm.; height 0·38 mm.

REMARKS. *Cytherelloidea refecta* has a distinctive ornamentation which separates it from other Jurassic species of the genus. Within the Jurassic the predominant ornamentation of the cytherelloideas consists of either a peripheral ridge or swelling and/or a central ridge or swelling. The development of strong lateral ridges extending from the posterior region, though present in some Jurassic species (Field 1966), is predominantly a feature of Cretaceous and Tertiary species.

Suborder PODOCOPINA Sars 1866

Superfamily **BAIRDIACEA** Sars 1888

Family **BAIRDIIDAE** Sars 1888

Genus ***BAIRDIA*** McCoy 1844

Bairdia hilda Jones

(Pl. 4, fig. 5)

1884 *Bairdia hilda* Jones : 771, pl. 34, fig. 20.
1888 *Bairdia fullonica* Jones & Sherborn : 253, pl. 5, figs. 4*a–c*.

For complete synonymy see p. 383.

REMARKS. Sylvester-Bradley (1948 : 199) first pointed out that the variation found within specimens of *Bairdia hilda* and *Bairdia fullonica* was such that there was as yet no evidence for regarding these species as distinct. Accordingly they were placed in synonymy. The lectotype of *B. fullonica* (I.1873, a right valve from the Blue Fuller's Earth Clay, figured Jones & Sherborn) was in the Jones & Sherborn Collection, whilst the paralectotype, also a right valve (Io.3554) and from the Blue Fuller's Earth Clay, was in the Winwood Collection.

DIMENSIONS. I.1873, right valve, length 0·79 mm.; height 0·42 mm. Io.3554, right valve, length 0·76 mm.; height 0·39 mm.

In addition to the types there are four right valves and one left valve (I.1848 from the Jones & Sherborn Collection and Io.3911–2 and Io.271 from the Winwood Collection) from the Blue Fuller's Earth Clay and referred to by Jones & Sherborn on p. 253.

Bairdia sherborni sp. nov.

(Pl. 6, fig. 8; Pl. 7, fig. 1)

Diagnosis. Carapace sub-rectangular in outline. Dorsal margin very slightly convex, sloping slightly to posterior. Ventral margin strongly incurved medially. Anterior end obliquely rounded. Posterior end narrowly rounded, somewhat tapering, but not upturned. Left valve larger than the right. Muscle scars as for the genus. Shell surface strongly and coarsely pitted.

Holotype. Io.3913, complete carapace from the Yellow Fuller's Earth Clay, Winwood Collection.

Paratype. Io.3557, complete carapace from the Fuller's Earth Clay, Möckler Collection.

Description. Carapace sub-rectangular, elongate bairdioid in outline, the dorsal margin very slightly convex but almost straight, sloping gently to the posterior. The ventral margin is typical of the genus, being strongly incurved medially. Anteriorly the margin is obliquely rounded, sharply cut just above a line running through mid-point (line of greatest length) by the inclined antero-dorsal slope. Postero-dorsal slope slightly concave, postero-ventral slope convex. Posterior end tends to be tapered without the strong upturning of most bairdias. Greatest height of carapace through the anterior cardinal angle; greatest width in the posterior third. Shell surface distinctly and evenly pitted. Left valve larger than the right which it overlaps mid-ventrally though not antero-ventrally and postero-ventrally. Antero-dorsally and postero-dorsally the gape is replaced by a prominent overlap of the right valve by the left. Internal details not observed apart from the **muscle scars** which may be observed as impressions on the internal cast of the holotype. They comprise seven adductor scars arranged in a circle with an eighth situated at the centre and a ninth, probably also an adductor scar, situated dorsally to this group. An additional dorsal scar is placed above that last mentioned whilst antero-ventrally there are two oval "mandibular" scars and antero-dorsally a single "antennal" scar.

Dimensions. Io.3913, carapace, length 0·58 mm.; height 0·31 mm.; width 0·21 mm. Io.3557, carapace, length 0·71 mm.; height 0·39 mm.; width 0·27 mm.

Remarks. Only two specimens have been found, one in each of two major collections. The outline of the carapace; obvious antero-ventral and postero-ventral gape and distinct surface pitting distinguish this species easily from all other Jurassic bairdiids.

Superfamily **CYPRIDACEA** Baird 1845

Family **PARACYPRIDIDAE** Sars 1923

Genus ***PARACYPRIS*** Sars 1866

Paracypris terraefullonicae (Jones & Sherborn)

(Pl. 7, figs. 2, 4)

1888 *Macrocypris terrae-fullonicae* Jones & Sherborn : 252, pl. 5, figs. 3*a–c*.
1888 *Macrocypris horatiana* Jones & Sherborn : 252, pl. 5, figs. 2*a–c*.
1967 *Paracypris terraefullonica* (Jones & Sherborn) Bate : 27, pl. 1, figs. 1–6.

Diagnosis. Carapace elongate, posteriorly acuminate. Anterior end rounded. Ventral margin almost straight in the larger left valve, more strongly concave in the right. Dorsal margin arched with antero-dorsal slope tending to be slightly concave, more noticeably so in the right valve. Shell surface smooth. Anterior and posterior vestibules well-developed. Radial pore canals branching.

Lectotype. I.1875, left valve, figured Jones & Sherborn 1888, pl. 5, figs. 3*a–c*, from the Blue Fuller's Earth Clay.

Other material. I.1874, right valve (lectotype of *Macrocypris horatiana* Jones & Sherborn), figured Jones & Sherborn 1888, pl. 5, figs. 2*a–c*, and Io.3548–53 (paralectotypes of *M. horatiana* and *M. terraefullonicae*), from the Blue Fuller's Earth Clay.

Remarks. *Paracypris terraefullonicae* has been fully described in Bate (1967 : 27). The additional specimens listed above (Io.3548–53) were found in the Winwood Collection and are paralectotypes of *Macrocypris horatiana* and *Macrocypris terraefullonicae* which " species " are the right and left valves respectively of *Paracypris terraefullonicae*.

Dimensions. I.1875, left valve, length 0·60 mm.; height 0·28 mm. I.1874, right valve, length 0·58 mm.; height 0·26 mm.

Superfamily **CYTHERACEA** Baird 1850

Family **BYTHOCYTHERIDAE** Sars 1926

Genus ***MONOCERATINA*** Roth 1928

Monoceratina visceralis (Jones & Sherborn)

(Pl. 7, fig. 3)

1888 *Cytheridea visceralis* Jones & Sherborn : 268, pl. 3, figs. 6*a–c*.

Diagnosis. Carapace sub-rectangular in outline with rounded anterior end; the antero-dorsal margin tends to curve obliquely backwards. Posterior end triangular with greatest prolongation situated in dorsal half of valve. Dorsal and ventral margins parallel. A distinct median sulcus present in dorsal half of valve only.

Valve convex, prominently swollen in postero-ventral region. Shell surface strongly pitted. Postero-ventral margin slightly serrated. Hinge with strong, straight, median bar.

Holotype. I.1830, left valve, figured Jones & Sherborn 1888, from the Blue Fuller's Earth Clay.

Description. The carapace is sub-rectangular in outline with a triangular posterior end, the ventral margin of which is longer than the straight postero-dorsal margin, and is evenly serrated along its length. At the postero-ventral angle there is a distinct convexity of the margin. Anterior cardinal angle prominently rounded. Dorsal and ventral margins parallel. A distinct vertical median sulcus is present in the dorsal half of the valve only. Carapace strongly swollen along the ventro-lateral border and postero-ventrally where the swelling is strongly undercut. Shell surface coarsely pitted, the pits extending uniformly over the valve. Line of greatest length lies above mid-point, whilst the line of greatest height passes approximately through the centre of the valve. Internally the hinge has been damaged, only the posterior part of the strong hinge bar being present. No other internal details observed.

Dimensions. I.1830, left valve, length 0·66 mm.; height 0·30 mm.

Remarks. Only the holotype is known, but it is distinct from the other species of *Monoceratina* described from the Jurassic. *M. visceralis* is close to *M. vulsa* (Jones & Sherborn), although the latter has a much coarser ornamentation, almost reticulate, whilst the median sulcus is much more strongly developed, as is the under-cutting of the ventro-lateral and postero-ventral swelling. *M. vulsa* is also distinguished by possessing a distinct furrow paralleling the anterior margin. *M. ungulina* Triebel & Bartenstein (1938, pl. 1, figs. 3, 4) may be distinguished on outline, the posterior extremity being situated higher up on the valve because of the shorter postero-dorsal slope. The anterior margin is also uniformly rounded with a flattened marginal border.

Monoceratina vulsa (Jones & Sherborn)

(Pl. 7, fig. 5)

1888 *Cytheridea vulsa* Jones & Sherborn : 263, pl. 2, figs. 4*a*, *b*.
1938 *Monoceratina vulsa* (Jones & Sherborn) Triebel & Bartenstein : 516, pl. 3, figs. 17, 18.
1960 *Monoceratina* cf. *vulsa* (Jones & Sherborn); Lutze : 433, pl. 37, figs. 5*a*, *b*.
?1963 *Monoceratina* sp. juv. aff. *vulsa* (Jones & Sherborn); Plumhoff : 48, pl. 11, figs. 167, 168.
1963 *Monoceratina vulsa* (Jones & Sherborn); Bate : 189, pl. 3, figs. 5–12.
1963*a* *Monoceratina vulsa* (Jones & Sherborn); Bate : 26, pl. 1, fig. 6.
1964 *Monoceratina vulsa* (Jones & Sherborn); Bate : 9.

Diagnosis. Shell sub-rectangular in lateral view, convex in dorsal view. Vertical median sulcus deeply incised, surrounded below and to the sides by a prominent swelling which is strongly undercut ventro-laterally. Lateral swelling separated from anterior margin by a furrow which runs parallel to that margin. Shell surface strongly pitted, the raised borders of the pits giving the surface a wrinkled appearance.

Lectotype. I.1842, a badly damaged left valve, figured Jones & Sherborn 1888, from the Blue Fuller's Earth Clay.

Remarks. Only a single damaged valve remains of the two specimens originally placed in this species by Jones & Sherborn (p. 263), and this is the figured specimen. A complete description was given by Bate (1963) who incorrectly recorded the lectotype as coming from the Richmond boring.

Dimensions. I.1842, length 0·64 mm.; height 0·32 mm. Both measurements would have been slightly larger if the specimen had not suffered slight damage posteriorly and along the dorsal margin.

Family **TRACHYLEBERIDIDAE** Sylvester-Bradley 1948

Subfamily **TRACHYLEBERIDINAE** Sylvester-Bradley 1948

Genus ***OLIGOCYTHEREIS*** Sylvester-Bradley 1948

Oligocythereis fullonica (Jones & Sherborn)

(Pl. 7, fig. 6)

1888 *Cythereis fullonica* Jones & Sherborn : 256, pl. 4, figs. 13*a–c*.
1948 *Cythereis* cf. *fullonica* Jones & Sherborn; Sylvester-Bradley : 186, pl. 12, figs. 7, 8 [not figs. 9, 10], pl. 13, fig. 3 [not fig. 9].
1948*a* *Oligocythereis fullonica* (Jones & Sherborn) Sylvester-Bradley : 796.
1963 *Oligocythereis fullonica* (Jones & Sherborn); Oertli : 39, pl. 25, fig. *a*?, pl. 29, fig. *a*, [not pl. 24, fig. *a*, pl. 26, fig. *a*].
1967 *Oligocythereis fullonica* (Jones & Sherborn); Bate : 61, pl. 21, fig. 14, [not fig. 15].

Diagnosis. Carapace subquadrate in outline with a broadly rounded anterior and broadly triangular posterior end. Anterior and posterior margins with small denticles. Ventral surface flattened, V-shaped in outline; ventral margin gently convex anteriorly and posteriorly. Dorsal margin almost straight, approximately paralleling ventral margin. Anterior cardinal angle extremely prominent with a large, rounded eye tubercle below. A short, thick ridge extends obliquely antero-ventrally from eye tubercle. Dorso-median ridge extends back from eye tubercle, enlarging posteriorly to give carapace triangular outline in dorsal view. Termination of dorso-median ridge produces a sharply pointed tubercle, angular in outline, the two sides of which are at right angles. Postero-ventrally a short, raised ridge almost vertically directed bends round at an oblique angle to extend forwards ventro-laterally bending upwards antero-ventrally to terminate in a prominent tubercle. This ventro-lateral ridge describes a broadly crescentic outline around a prominent, irregular tubercle. Prominent tubercle developed slightly anterior of mid-point. Shell surface very finely punctate. Left valve larger than right.

Lectotype. I.1871, complete carapace, figured Jones & Sherborn 1888, from the Blue Fuller's Earth Clay.

Description. Carapace subquadrate in outline, ornamented as diagnosed. The angular outline of the shell is produced dorsally by the prominent antero-dorsal

eye tubercle and the strong postero-dorsal tubercle and ventrally by the postero-ventral and antero-ventral terminations of the ridge which extends along the ventro-lateral margin. The large tubercle situated slightly anterior of mid-point is the **muscle scar node** characteristic of the family. The anterior and posterior margins possess small denticles whilst the marginal borders bear a few additional nodes. Shell surface finely punctate. In dorsal view the outline of the carapace in the median part is V-shaped as is the ventral surface. This outline is produced by the dorso-median and ventro-lateral ridges diverging slightly towards the posterior end. Left valve larger than the right which it overlaps along the ventral margin and in the region of the cardinal angles and overreaches along the postero-dorsal slope. Internal details not observed in the type material, but the entomodont type **hinge** has been described by Sylvester-Bradley (1948 : 187).

DIMENSIONS. Lectotype, I.1871, carapace, length 0·54 mm.; height 0·32 mm.; width 0·27 mm.

REMARKS. Sylvester-Bradley (1948 : 187) noted variation within the ornamentation of specimens which he placed in *O. fullonica* (Jones & Sherborn), and it has been current practise to retain these within the species. The forms possessing a postero-dorsal tubercle from which three arms radiate (see Sylvester-Bradley 1948, pl. 12, figs. 9, 10) should be assigned to a new species. *O. fullonica* should be retained only for those specimens in which the postero-dorsal tubercle has two arms at right angles, and in which the muscle scar node to the centre of the valve is completely isolated and not joined to the anterior termination of the ventro-lateral ridge.

Family **SCHULERIDEIDAE** Mandelstam 1959

Subfamily **SCHULERIDEINAE** Mandelstam 1959

Genus ***SCHULERIDEA*** Swartz & Swain 1946

Subgenus ***EOSCHULERIDEA*** Bate 1967

Schuleridea* (*Eoschuleridea*) *horatiana (Jones & Sherborn)

(Pl. 7, fig. 7; Text-fig. 5)

1888 *Cytheridea horatiana* Jones & Sherborn : 263, pl. 2, figs. 5*a*, *b*.

DIAGNOSIS. Carapace oval/elongate, anteriorly rounded, posteriorly tapering, narrowly rounded. Greatest length of carapace below mid-point, greatest height at anterior cardinal angle. Elongate eye swelling with groove beneath present in right valve below anterior cardinal angle. Left valve projects slightly above right just behind anterior cardinal angle. Shell surface punctate with widely scattered, large, normal pore canals. Twenty-five to thirty radial pore canals splayed fan-like around anterior margin. Muscle scars type C. Hinge paleomerodont.

LECTOTYPE. I.1852, male right valve, figured Jones & Sherborn 1888, from the Blue Fuller's Earth Clay.

PARALECTOTYPE. Io.3940, male carapace from Blue Fuller's Earth Clay, Winwood Collection.

DESCRIPTION. Carapace oval/elongate in outline with uniformly rounded anterior margin and narrowly rounded, tapered posterior. The line of greatest length passes well below the mid-point. Greatest height at the anterior cardinal angle, greatest width just behind the mid-point. Dorsal margin convex, slightly umbonate in the left valve just behind the anterior cardinal angle. Ventral margin convex with an antero-median incurvature. Shell surface punctate with widely scattered, large, rounded, normal pore canals. An elongate **eye swelling** is situated below the anterior cardinal angle in the right valve and has an oblique furrow situated beneath. **Muscle scars** as viewed externally of type **C** (Bate 1963). Anterior **radial pore canals** splayed fan-like around the anterior margin, largely concentrated below mid-height, approximately twenty-five to thirty in number. **Hinge** paleomerodont as seen in the right valve. Terminal teeth larger anteriorly, where there are five, than posteriorly, where there are eight. Median bar smooth. Left valve larger than right. Inner margin and line of concrescence coincide, anterior duplicature broad.

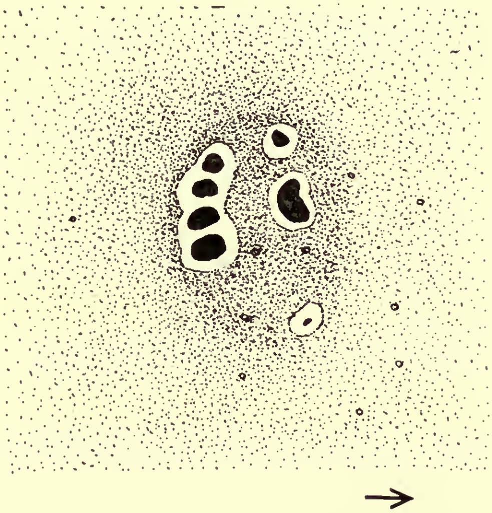


FIG. 5. Muscle scars, × 200. *Schuleridea* (*Eoschuleridea*) *horatiana* (Jones & Sherborn), lectotype, I.1852.

DIMENSIONS. I.1852, right valve, length 0·85 mm.; height 0·46 mm. Io.3940, carapace, length 0·79 mm.; height 0·46 mm.; width 0·36 mm.

REMARKS. Both available specimens of this species are male dimorphs as indicated by their shell outline. No female dimorph has been recognized. This species is very close to the male dimorph of *Schuleridea* (*Eoschuleridea*) *bathonica* Bate (1967) although the latter has fewer anterior radial pore canals and does not have the line of greatest length as ventrally positioned as in *horatiana*. Male dimorphs of *Schuleridea* species are notoriously alike and extremely difficult to tell apart. Until a female dimorph has been identified for *horatiana* from the Fuller's Earth it is preferred to regard these two species as distinct.

Genus *ASCIOCYTHERE* Swain 1952

Asciocythere obovata (Jones & Sherborn)

(Pl. 7, fig. 8; Pl. 8, figs. 2, 3, 7; Text-fig. 6)

1888 *Cytheridea obovata* Jones & Sherborn : 264, pl. 2, figs. 6*a–c*.

DIAGNOSIS. Carapace oval in lateral view, strongly convex in dorsal view. Dorsal margin broadly arched, curving down into well-rounded anterior and more narrowly rounded posterior margin without change in slope at cardinal angles. Ventral margin broadly convex. Line of greatest length slightly below mid-point. Shell surface very finely punctate.

LECTOTYPE. I.1836, right valve, figured Jones & Sherborn 1888, pl. 2, figs. 6*a–c*, from the Yellow Fuller's Earth Clay.

PARALECTOTYPE. Io.3938, carapace from the Yellow Fuller's Earth Clay, Winwood Collection.

OTHER MATERIAL. Io.3939, left valve from the Blue Fuller's Earth Clay, Winwood Collection.

DESCRIPTION. Carapace oval in outline with strongly arched dorsal margin and indistinct cardinal angles, the dorsal margin curving down without a break into the rounded anterior margin and the more narrowly rounded posterior margin. Ventral margin broadly convex. Shell surface appears smooth but is in fact very finely punctate. Greatest length of carapace just below mid-point. Greatest height median; greatest width just behind mid-point. Left valve larger than right, overlapping the right along the ventral, posterior and postero-dorsal slopes. Antero-dorsally and anteriorly the valves tend to gape and there is no overlap. **Hinge** antimerodont: right valve with ten dorsally bifid anterior teeth and nine dorsally bifid posterior teeth. Median groove very short and loculate. Left valve hinge not seen. Inner margin and line of concrescence coincide, duplicature strongly developed. Anterior **radial pore canals** widely spaced and only very slightly curved, almost straight, sixteen in number. **Muscle scars** not observed.

DIMENSIONS. I.1836, right valve, length 0·54 mm.; height 0·34 mm.; Io.3938, carapace, length 0·49 mm.; height 0·35 mm.; width 0·30 mm. Io.3939, left valve, length 0·62 mm.; height 0·42 mm.

REMARKS. Only two species of *Asciocythere* have been described from the British Middle Jurassic so far; *A. lacunosa* Bate 1963*a* and *A. acuminata* Bate 1964, both from the Bajocian. The present species, the first to be described from the Bathonian, is not so posteriorly acuminate as *A. acuminata* and not so strongly pitted as *A. lacunosa*.

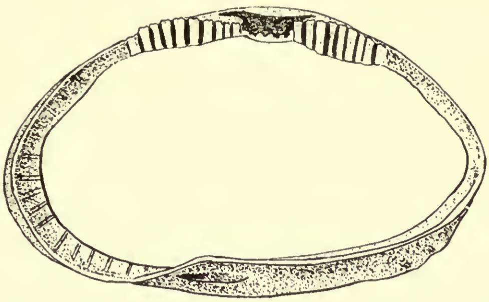


FIG. 6. *Asciocythere obovata* (Jones & Sherborn). Internal view, right valve, lectotype, I.1836. × 115.

Genus *PRAESCHULERIDEA* Bate 1963

Praeschuleridea subtrigona subtrigona (Jones & Sherborn)

(Pl. 8, figs. 4–6)

1888 *Cytheridea subtrigona* Jones & Sherborn : 265, pl. 2, figs. 9*a–c*.
1963 *Praeschuleridea subtrigona* (Jones & Sherborn) Bate : 207, pl. 12, figs. 12–16, pl. 13, figs. 1–9.
1963*a* *Praeschuleridea subtrigona* (Jones & Sherborn); Bate : 41.
1964 *Praeschuleridea subtrigona subtrigona* (Jones & Sherborn); Bate : 22.
1965 *Praeschuleridea subtrigona subtrigona* (Jones & Sherborn); Bate : 124.

DIAGNOSIS. Carapace oval-subtrigonal in outline, punctate. Length of adult of the order of (female) 0·56 mm.; (male) 0·58 mm.

LECTOTYPE. I.1838, male right valve, not the figured specimen of Jones & Sherborn, which was of a left valve. Blue Fuller's Earth Clay.

PARALECTOTYPES. Io.3935–7, female and two male carapaces, Blue Fuller's Earth Clay, Winwood Collection.

REMARKS. *Praeschuleridea subtrigona* is the type species of the genus and as such has been described fully in earlier publications. Three subspecies are recognized so far, *subtrigona subtrigona* being the smallest and having the longest stratigraphical range: Middle Bajocian (*Sonninia sowerbyi* Zone, *Hyperlioceras discites* Subzone) to Upper Bathonian (*Prohecticoceras retrocostatum* Zone). The other two subspecies, *P. subtrigona magna* Bate (1964) and *P. subtrigona intermedia* Bate (1965), have much shorter ranges and are restricted to the Bajocian. The measurements of the type specimens have not previously been given and are included here.

DIMENSIONS. I.1838, male right valve, length 0·53 mm.; height 0·32 mm. Io.3935, male carapace, length 0·55 mm.; height 0·37 mm.; width 0·29 mm. Io.3936, male carapace, length 0·54 mm.; height 0·36 mm.; width 0·29 mm. Io.3937, female carapace, length 0·50 mm.; height 0·35 mm.; width 0·30 mm. Comparison of the above measurements with those given in Bate (1963 : 209) shows that the size of the *P. subtrigona subtrigona* has remained stable since the Bajocian.

Genus *EOCYTHERIDEA* Bate 1963

Eocytheridea sp.

(Pl. 8, fig. 1)

Remarks. Known from a single right valve, possibly of a male dimorph (Winwood Collection). The surface of the valve is strongly pitted by rather broad pits which, towards the centre of the valve, produce a reticulation but in the antero-dorsal and postero-dorsal areas are elongated obliquely towards the centre of the dorsal margin. This elongation produces a series of ridges which radiate down from the centre of the dorsal margin. The ornamentation readily distinguishes this species from *Eocytheridea faveolata* Bate (1964) which has a more uniform reticulate ornamentation without the development of obliquely radiating ridges in the dorsal part of the carapace. The hinge is hemimerodont. Twelve long, slightly curved anterior radial pore canals pass through the broad duplicature.

This is the first record of the genus outside the Bajocian

Dimensions. Io.3906, right valve, length 0·77 mm.; height 0·36 mm.

Family **CYTHERIDEIDAE** Sars 1925

Subfamily **CYTHERIDEINAE** Sars 1925

Genus *HADROCYTHERIDEA* nov.

Derivation of name. *hadros*, Gr., well developed + *cytheridea*.

Diagnosis. Carapace robust, expanded posteriorly in both width and height. Hinge straight, antero-dorsal and postero-dorsal slopes steeply angled. Anterior end rounded, posterior end triangular in elongate male dimorph. Female with triangular posterior end, slightly upturned. Line of greatest length lower in female dimorph. Postero-ventral part of carapace characteristically swollen, particularly in the female. Hine antimerodont. Inner margin and line of concrescence coincide; duplicature broad. Anterior radial pore canals long, straight, widely and uniformly spaced, nine in the type species. In front of a vertical row of four small, oval adductor scars, there is a bill-hook or broadly heart-shaped antero-dorsal antennal scar and a small antero-ventral mandibular scar. Left valve larger than the right. Shell surface coarsely pitted.

Type species. *Cytheridea dolabra* Jones & Sherborn 1888.

Remarks. This new genus has been placed in the Cytherideidae on the basis of carapace morphology and muscle scar pattern. It is easily recognizable by its rectangular/quadrate outline, postero-ventral convexity and position of greatest height and width towards the posterior. The outline of the male dimorph is to some extent reminiscent of *Fabanella* Martin 1961, but that of the female is completely different.

Hadrocytheridea dolabra (Jones & Sherborn)

(Pl. 9, figs. 1–8; Pl. 10, fig. 1; Text-fig. 7)

1888 *Cytheridea dolabra* Jones & Sherborn : 267, pl. 3, figs. 3*a–c*.
1888 *Cytheridea puteolata* Jones & Sherborn : 259, pl. 1, figs. 7*a–c*.
1888 *Cytheridea parallela* Jones & Sherborn : 260, pl. 1, figs. 9*a–c*.
1888 *Cytheridea pentagonalis* Jones & Sherborn : 261, pl. 2, figs. 1*a–c*.
1888 *?Cytheridea ignobilis* Jones & Sherborn : 268, pl. 3, figs. 9*a–c*.

DIAGNOSIS. *Hadrocytheridea* with robust dimorphic carapace. Shell surface finely punctate between distinct circular pits, at the centre of which is a large, circular normal pore canal opening. Other details as for genus.

LECTOTYPE. I.1851, female right valve, figured Jones & Sherborn 1888, pl. 3, figs. 3*a–c*. Blue Fuller's Earth Clay, Midford.

PARALECTOTYPES. I.1844, male left valve, figured Jones & Sherborn 1888, pl. 1, figs. 7*a–c*. This specimen was described by Jones & Sherborn as *Cytheridea puteolata* and is selected here as lectotype of that species. Additional paralectotypes of *C. puteolata* are Io.3921–2 from the Winwood Collection.

I.1859, male carapace, figured Jones & Sherborn 1888, pl. 1, figs. 9*a–c*. This was described as *Cytheridea parallela* and is here selected as lectotype of that species. Additional paralectotypes of *C. parallela* are Io.3924–8 from the Winwood Collection.

I.1866, female left valve, figured Jones & Sherborn 1888, pl. 2, figs. 1*a–c*. This is the holotype of *Cytheridea pentagonalis*.

All the above paralectotypes of *Hadrocytheridea dolabra* apart from I.1866, which comes from the Yellow Fuller's Earth Clay, come from the Blue Fuller's Earth Clay of Midford, near Bath.

OTHER MATERIAL. Jones & Sherborn (1862 : 262) stated that *Cytheridea pentagonalis* was represented by a single specimen only. Two single right valves of this species, Io.273 and Io.3929, also occur in the Winwood Collection from the Blue Fuller's Earth Clay but cannot be regarded as paralectotypes.

DESCRIPTION. Carapace quadrate with sharply angled, prominent cardinal angles and steeply sloping antero- and postero-dorsal slopes in the female dimorph, elongate, more rectangular in outline in the male. Dorsal margin straight, ventral margin medially incurved. Anterior end broadly rounded in the left valve, truncated dorsally in the right by the steeply sloping antero-dorsal slope. In the queried juvenile right valve this truncation of the anterior margin is not present. Posterior end triangular, the postero-dorsal slope strongly concave in the female, resulting in a distinct upturning of the posterior end in both valves but more strongly so in the right. In the male this upturning is restricted to the right valve. Greatest length of carapace below mid-point in both dimorphs but more ventrally situated in the female. Greatest height and width developed in the posterior third of the carapace. In the male the increase in width posteriorly is uniformly developed in that area. In the female the increase in width tends to be restricted to the postero-ventral region. Left valve larger than the right, with the left overlapping the right along the ventral

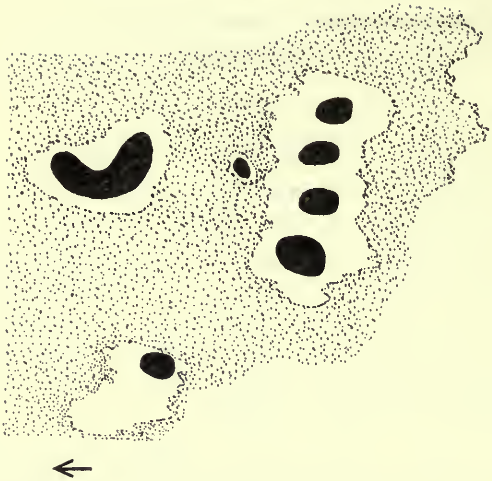


FIG. 7. *Hadrocytheridea dolabra* (Jones & Sherborn). Muscle scars of lectotype of *Cytheridea puteolata* Jones & Sherborn, from the exterior. I.1844. × 500.

margin. Elsewhere there does not appear to be any overlap. Shell surface very finely punctate in between the large circular pits, each of which has a large normal pore canal opening at its centre. **Hinge** antimerodont, strongly developed with five anterior and five posterior teeth. Median groove loculate. Inner margin and line of concrescence coincide to produce a broad duplicature through which pass (anteriorly) nine, long, straight and widely-spaced **radial pore canals. Muscle scars** consist of a vertical row of four small, oval adductor scars, a small, round antero-ventral mandibular scar and a large antero-dorsal antennal scar which is equal in size to two adductor scars and is either heart-shaped or bill-hooked in outline.

DIMENSIONS. I.1851, female right valve, length 0·64 mm.; height 0·38 mm. I.1844, male left valve, length 0·71 mm.; height 0·34 mm. I.1859, male carapace, length 0·73 mm.; height 0·36 mm.; width 0·37 mm. I.1866, female left valve, length 0·57 mm.; height 0·32 mm. Io.3294, male right valve, length 0·65 mm.; height 0·31 mm. I.1868, ?juvenile right valve, length 0·46 mm.; height 0·26 mm.

REMARKS. Jones & Sherborn (1888) described four different species which were either male or female dimorphs of a single species. Although *Cytheridea puteolata* had page preference it was decided to select a female dimorph as type because it is the female outline which is continuous with juvenile instars. Of the two female specimens available, that identified as *Cytheridea dolabra* was the better preserved and was therefore chosen to identify the species. The breakdown of the synonymous species is as follows:

Female right valve . .	*Cytheridea dolabra*
Female left valve . . .	*Cytheridea pentagonalis*
Male carapace . . .	*Cytheridea parallela*
Male left valve . . .	*Cytheridea puteolata*
?Juvenile instar . . .	*Cytheridea ignobilis*

Hadrocytheridea dolabra is close to *Cytheridea punctiputeolata* Jones & Sherborn, as far as the male right valve is concerned, but *C. punctiputeolata* has a lophodont hinge, more rounded posterior end and a more strongly developed ornamentation of punctae and pits. *Cytheridea ignobilis* has been included in this species as it probably represents a juvenile instar. However, because of the slight difference between the anterior margin of *C. ignobilis* and that of *H. dolabra* and the absence of other juveniles to establish an ontogentetic sequence, *C. ignobilis* is doubtfully referred to this species and is not placed in the list of paralectotypes.

Family **PROGONOCYTHERIDAE** Sylvester-Bradley 1948

Subfamily **PROGONOCYTHERINAE** Sylvester-Bradley 1948

Genus ***RECTOCYTHERE*** Malz 1958

Rectocythere sugillata (Jones & Sherborn)

(Pl. 10, figs. 3–6)

1888 *Cytheridea sugillata* Jones & Sherborn : 262, pl. 2, figs. *2a–c*.

DIAGNOSIS. *Rectocythere* with surface ornamentation of irregular ridges and raised areas giving parched or shrivelled-up appearance. Coarsely pitted in well-preserved specimens.

LECTOTYPE. I.1855, left valve figured Jones & Sherborn 1888. Blue Fuller's Earth Clay, Midford.

PARALECTOTYPE. Io.3930, right valve referred to by Jones & Sherborn 1888 : 262, Blue Fuller's Earth Clay, Winwood Collection.

DESCRIPTION. Shell robust, with high anterior and posteriorly sloping dorsal margin. Anterior end broadly rounded; posterior end narrowly rounded in the left valve, triangular in the right, with a concave postero-dorsal slope producing an upturned posterior end. Ventral margin slopes upwards towards the posterior end, but is over-hung postero-ventrally by the prominent convexity of the ventro-lateral margin in that region. Anterior and posterior marginal borders flattened, the convex central part of the carapace is strongly ornamented by irregular ridges and raised areas which give a dehydrated appearance to the ostracod. **Hinge** lophodont. Inner margin and line of concrescence coincide producing a rather broad duplicature. To the outside of this there is developed a narrow flange extending around the anterior margin and along the ventral margin to the apex of the posterior end. Anterior **radial pore canals** long and straight, widely spaced and about seven to eight in number. **Muscle scars** not observed.

DIMENSIONS. I.1855, left valve, length 0·50 mm.; height 0·31 mm. Io.3930, right valve, length 0·51 mm.; height 0·32 mm.

REMARKS. *Rectocythere sugillata* possesses the same basic ornamentation as *R. rugosa* Malz (1966*a* : 405, figs. 6–9) but may be distinguished by having a much finer degree of surface pitting and additional irregular swellings. Dr. Malz kindly sent material of *R. rugosa* for comparison.

The ostracod *Camptocythere lincolnensis* Bate (1963 : 201, pl. 10, figs. 2–13) also belongs to *Rectocythere* on its similarity of carapace outline, ornamentation and internal details.

Genus *CAYTONIDEA* Bate 1965

DIAGNOSIS. Progonocytherinae, oval-rectangular in outline with well-rounded anterior and posterior margins. Low eye swelling situated at anterior cardinal angle. Cardinal angles prominent, broadly rounded. Shell surface with reticulate ornamentation. Hinge antimerodont. Muscle scars consist of subvertical row of four adductor scars, rounded antero-dorsal antennal scar and rounded antero-ventral mandibular scar. Radial pore canals long, straight, few in number. Left valve larger than right. Dimorphic.

REMARKS. Since the publication of this genus a second species has been identified which enables some modification to the diagnosis to be made. This concerns the identification of dimorphism and the determination of a reticulate ornamentation as a constant feature.

A re-examination of the type species, *Caytonidea faveolata* Bate (1965 : 100, pl. 1, figs. 13–14, pl. 2, figs. 1–10), has shown that the holotype (Io.1831) is a female dimorph and the paratype (Io.1834) a male.

Caytonidea terraefullonicae (Jones & Sherborn)

(Pl. 10, figs. 2, 7, 8; Pl. 11, figs. 1–3)

1888 *Cytheridea terrae-fullonicae* Jones & Sherborn : 258, pl. 1, figs. 5*a–c*.

DIAGNOSIS. *Caytonidea* with coarse reticulate ornamentation of five- to six-sided pits covering entire shell surface. Extreme postero-ventral margin swollen, slightly overhanging ventral surface. Males more elongate in outline than females.

LECTOTYPE. I.1869, left valve, figured Jones & Sherborn 1888. Blue Fuller's Earth Clay, Midford.

PARALECTOTYPES. Io.3917–20, male and female specimens from the Winwood Collection, Blue and Yellow Fuller's Earth Clay, Midford.

OTHER MATERIAL. Io.4002–3, right valve and juvenile carapace from the J. F. Blake Collection, Fuller's Earth Clay, Bath.

DESCRIPTION. Carapace rectangular in outline, especially in the male dimorph, with sub-parallel dorsal and ventral margins. Anterior end high with greatest height through the anterior cardinal angle which is situated close to the anterior margin. Anterior end broadly but slightly obliquely rounded and extended ventrally below the ventral margin. Posterior end broadly rounded in the left valve, with oblique postero-dorsal slope in the right valve. Postero-ventral margin slightly swollen and overhanging ventral surface. Greatest length of carapace passes slightly below the mid-point; greatest width in the posterior third. There are no marginal borders. Left valve slightly larger than the right which it overlaps along the ventral margin but very little elsewhere. Shell surface coarsely reticulate, the reticulations producing five- to six-sided pits which cover the entire shell surface. In the juvenile carapace, the reticulations tend to form longitudinal ridges along the ventral surface. **Normal pore canals** large and widely spaced over the surface of the carapace. Inner margin and line of concrescence coincide to produce a broad duplicature through which pass a small number (about seven) of long, straight, and widely spaced anterior **radial pore canals**. A narrow flange extends around the anterior and ventral margins and along the postero-ventral part of the posterior margin. **Hinge** antimerodont, the median element being long and finely denticulate/locellate. Terminal elements dentate/loculate. **Muscle scars** as seen from the exterior consist of a small, rounded antero-dorsal antennal scar and a vertical row of four rounded adductor scars (type **A**). An oval smooth area in the region of the anterior cardinal angle is indicative of an **eye swelling**. This feature is only clearly seen in the male dimorph.

DIMENSIONS. I.1869, female left valve, length 0·54 mm.; height 0·30 mm. Io.3919, female right valve, length 0·49 mm.; height 0·26 mm. Io.3917, male right valve, length 0·54 mm.; height 0·26 mm. Io.3918, male left valve, length 0·55 mm.; height 0·26 mm. Io.3920, female carapace, length 0·52 mm.; height 0·29 mm.; width 0·25 mm.

REMARKS. *Caytonidea terraefullonicae* differs from *C. faveolata* Bate in the possession of a much stronger reticulate ornamentation, straighter dorsal margin, and postero-ventral swelling slightly overlapping the ventral surface. Unfortunately, during the examination of this material Io.3918 was lost and Io.3917 damaged.

Genus ***ACANTHOCYTHERE*** Sylvester-Bradley 1956

Acanthocythere sphaerulata (Jones & Sherborn)

(Pl. 11, figs. 4–6)

1888 *Cythere sphaerulata* Jones & Sherborn : 253, pl. 1, figs. 6*a–c*.
1956 *Acanthocythere sphaerulata* (Jones & Sherborn) Sylvester-Bradley : 12, pl. 1, figs. 1–4.

DIAGNOSIS. As for Sylvester-Bradley 1956 : 12.

HOLOTYPE. I.1835, female carapace, length 0·52 mm.; height 0·31 mm.; width 0·31 mm. Figured Jones & Sherborn 1888. Blue Fuller's Earth Clay, Midford.

REMARKS. *Cythere sphaerulata* was made the type species of *Acanthocythere* (Sylvester-Bradley 1956), additional material indicating that the species was dimorphic. A misprint on p. 12 stated that the holotype was a male dimorph; it is, in fact, a female dimorph.

Genus ***FASTIGATOCYTHERE*** Wienholz 1967

Fastigatocythere juglandica (Jones)

(Pl. 12, fig. 3)

1888 *Cythere juglandica* var. *major* Jones & Sherborn : 255, pl. 4, figs. 2*a*, *b*.

REMARKS. The synonymy and diagnosis of this species are given on p. 389. The variety described by Jones & Sherborn, of which the specimen I.1872 is holotype was correctly placed in synonymy by Sylvester-Bradley (1948).

DIMENSIONS. I.1872, female left valve, length 0·74 mm.; height 0·49 mm.

Genus ***GLYPTOCYTHERE*** Brand & Malz 1962

Glyptocythere guembeliana (Jones)

(Pl. 3, fig. 2; Pl. 4, fig. 1)

1884 *Cythere guembeliana* Jones : 772, pl. 34, figs, 32, 33 [not fig. 31].
1888 *Cytheridea pulvinar* Jones & Sherborn : 266, pl. 3, figs. 2*a*–*c*.
1888 *Cytheridea trapezoidalis* Terquem, Jones & Sherborn : 270, pl. 4, figs. 1*a*, *b*.
1967 *Glyptocythere guembeliana* (Jones) Bate : 49, pl. 13, figs. 10–16, pl. 14, figs. 1–8.

REMARKS. This species has been described fully by me (Bate 1967) although I omitted to include the ostracod identified by Jones & Sherborn as *Cytheridea trapezoidalis* Terquem. This specimen is a juvenile instar of *G. guembeliana*. Although it has a well-developed ventro-lateral keel, the outline of the valve is typically juvenile in being strongly acuminate posteriorly. The hinge, in being antimerodont, reflects an early stage in the development of the adult entomodont hinge.

DIMENSIONS. I.1858, female right valve (*Cytheridea pulvinar*), length 0·82 mm.; height 0·47 mm. I.1840, juvenile right valve (*Cytheridea trapezoidalis*), length 0·54 mm.; height 0·30 mm.

Glyptocythere oscillum (Jones & Sherborn)

(Pl. 5, fig. 2; Pl. 12, fig. 2; Text-figs. 8, 9)

1888 *Cythere oscillum* Jones & Sherborn : 254, pl. 3, figs. 8*a*–*c*.
1888 *Cytheridea striblita* Jones & Sherborn : 268, pl. 3, figs. 7*a*–*c*.

DIAGNOSIS. Carapace strongly ornamented with series of grooves and irregular swollen areas: two lateral grooves developed, the first ventro-laterally, the second just above valve middle, both joined by narrow vertical groove passing between two swollen areas. Broad dorso-median sulcus extends down to median groove. Area below ventro-lateral groove alate in right valve, swollen in both valves. From posterior region, two swollen areas extend towards valve centre whilst two similar areas extend back from anterior region. Lower of anterior swollen area terminates in prominent swelling. Anterior and posterior swollen areas do not unite. Normal pore canals prominently displayed over carapace.

HOLOTYPE. I.1849, described, figured Jones & Sherborn (1888). Female right valve from the Blue Fuller's Earth Clay, Midford.

OTHER MATERIAL. Io.3943, male left valve, referred to Jones & Sherborn (1888). Winwood Collection. Blue Fuller's Earth Clay, Midford. This is the lectotype of *Cytheridea striblita* Jones & Sherborn. Io.3914–6, two male left valves and a male right valve, Winwood Collection, Blue Fuller's Earth Clay, Midford.

DESCRIPTION. Carapace subquadrate to sub-rectangular in outline, the more elongate specimens being the males. Greatest length through the mid-point in the male dimorph, below in the female right valve. Greatest height in the posterior third. Dorsal margin, in the left valve, concave in the region of the dorso-median sulcus, convex posteriorly. The dorsal margin of the right valve is strongly convex, especially in the female. Cardinal angles particularly well developed in the right valve, postero-dorsal slope concave in both valves, more especially so in the female right valve. Antero-dorsal slope broadly convex in the male, concave in the female right valve. Anterior end broadly rounded, posterior end triangular. Ventral margin antero-medially concave, posteriorly convex. Ventro-lateral margin of right valve becomes alate, extending below ventral surface. This feature does not appear to be so well developed in the left valve. Anterior and posterior marginal borders flattened. Shell surface ornamented as described in the diagnosis. Normal pore canal openings prominent and widely scattered over the carapace. **Hinge** with five to six terminal teeth in the right valve and a median loculate groove. In the left valve the terminal loculate sockets are separated by a median bar which is rather coarsely dentate, particularly in the anterior part. Although not as well developed as in some species the hinge is regarded as entomodont. Inner margin and line of concrescence coincide. Anterior **radial pore canals** long and straight, widely spaced, about ten in number. **Muscle scars** not seen.

DIMENSIONS. Lectotype, I.1849, female right valve, length 0·53 mm.; height 0·30 mm. Io.3943, male left valve, length 0·62 mm.; height 0·32 mm. Io.3916, male right valve, length 0·59 mm.; height 0·30 mm.

REMARKS. Jones & Sherborn identified the female specimens of the present species as *Cythere oscillum*; the males they placed in *Cytheridea striblita*. The figured specimen of the latter species has been lost but the lectotype of *C. striblita* was found in the Winwood Collection.

Glyptocythere rudimenta Brand & Malz (1962 and 1966) is similar to *G. oscillum* in ornamentation but differs in that the anterior and posterior swollen areas take the form of rather thin irregular ridges, not nearly so broad as in *oscillum*. A broad sulcus is developed in *oscillum* in the dorso-median area, but in *rudimenta* there is a series of irregular ridges radiating down from the dorsal margin. The shell outline in the right valve is noticeably different, the cardinal angles and the dorso-median extension of the dorsal margin being very much more prominently developed in *G. oscillum*. The similarities in ornamentation between the two species suggests a phylogenetic relationship which is supported by their stratigraphic position, *G. rudimenta* being found in the Upper Bajocian and *G. oscillum* in the Upper

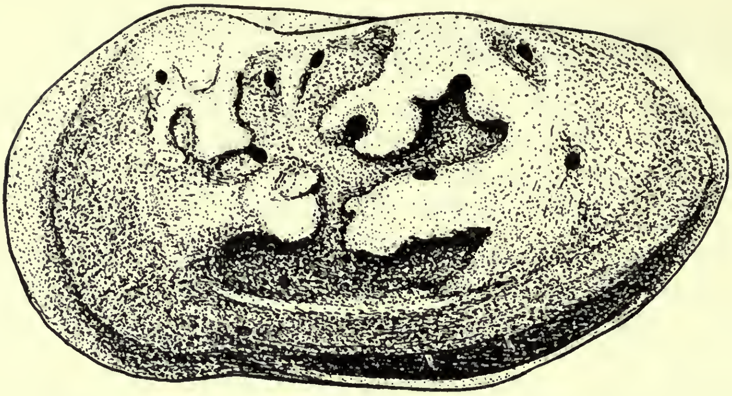


FIG. 8. *Glyptocythere oscillum* (Jones & Sherborn). Male left valve, paralectotype, Io.3943. × 153.

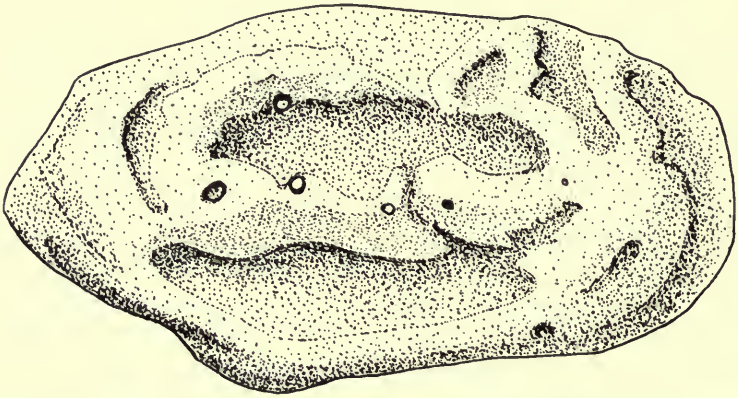


FIG. 9. *Glyptocythere oscillum* (Jones & Sherborn). Male right valve, Io.3916. × 165.

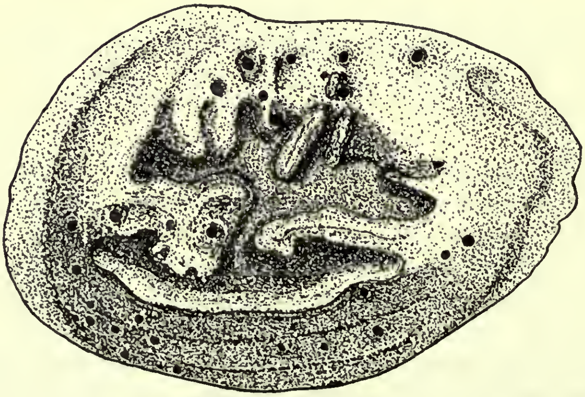


FIG. 10. *Glyptocythere rudimenta* Brand & Malz. Left valve, female carapace. Io.3921. × 113.

Bathonian. The kindness of Dr. D. E. Brand in sending me specimens of *G. rudimenta* is acknowledged here.

Glyptocythere persica (Jones & Sherborn)

(Pl. 12, fig. 1; Text-fig. 11)

1888 *Cytheridea persica* Jones & Sherborn : 270, pl. 4, fig. 4.

DIAGNOSIS. Carapace with broad dorso-median depression in anterior half; short, blade-like ventral keel on ventral surface and ventro-lateral margin develops into keel-like ridge. Lateral surface ornamented by neat reticulation. Ventral surface with low, longitudinal ridges. Anterior and posterior marginal borders smooth, compressed.

HOLOTYPE. I.1834, right valve, figured Jones & Sherborn (1888), Blue Fuller's Earth Clay, Midford.

OTHER MATERIAL. Io.4006, juvenile carapace, Möckler Collection, Fuller's Earth, Midford.

DESCRIPTION. Carapace with greatest height at the anterior end, through the anterior cardinal angle, tapering to the posterior end. Dorsal margin broadly convex, sloping to the posterior, ventral margin with a broad, median incurvature, below which in the right valve there is lip-like extension of the flange. The flange is continuous around the anterior margin and along the ventral margin to the tip of the triangular posterior end. Anterior end broadly rounded, posterior end with concave postero-dorsal slope and convex postero-ventral slope. Anterior and posterior marginal borders compressed and smooth, distinct from the more strongly convex part of the carapace which is ornamented by a neat reticulation. The ornamentation is extended along the ventro-lateral margin to form a keel-like ridge. Ventral surface ornamented by four longitudinal ridges, one of which is developed

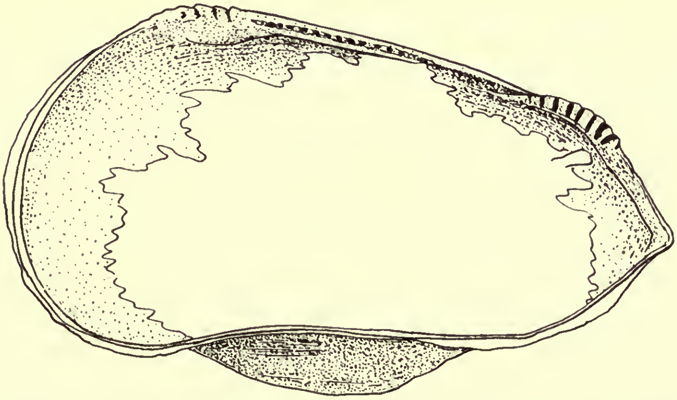


FIG. 11. *Glyptocythere persica* (Jones & Sherborn). Internal view of right valve. Holotype, I.1834. × 120.

into a short, blade-like keel. A smooth area at the anterior cardinal angle is suggestive of an ocular lens. Just anterior of valve centre and in the dorso-median part of the carapace a broad shallow sulcus is developed, especially noticeable in dorsal view. The posterior part of the valve behind the sulcus is noticeably more convex, whilst at the base of the sulcus, a raised area locates the position of the muscle scars. The left valve is larger than the right, which it overlaps along the ventral margin and slightly overreaches along the dorsal margin. The inner margin and line of concrescence coincide. The **hinge** is weakly entomodont.

DIMENSIONS. I.1834, right valve, length 0·70 mm.; height 0·38 mm. Io.4006, juvenile carapace, length 0·52 mm.; height 0·28 mm.; width 0·24 mm.

REMARKS. *Glyptocythere persica*, with its neat, reticulate ornamentation, distinct ventro-lateral ridge, and well-developed ventral, blade-like keel, is quite distinct from those species which possess well-developed ventro-lateral ridges or keels, e.g. *Glyptocythere costata* Bate (1965) and *G. guembeliana* (Jones) (Bate 1967), or from those which have a much stronger reticulate ornamentation, e.g. *Glyptocythere tuberodentina* Brand & Malz (1962*a*).

Genus ***LOPHOCYTHERE*** Sylvester-Bradley 1948

BRADIANA GROUP

Lophocythere acutiplicata (Jones & Sherborn)

(Pl. 1, fig. 8; Pl. 12, figs. 4, 6)

1888 *Cytheridea acutiplicata* Jones & Sherborn : 271, pl. 4, figs. *7a–b*, *8a–c*.

DIAGNOSIS. Carapace dimorphic, tapering posteriorly. Eye swelling below anterior cardinal angle. Shell surface weakly ornamented laterally, the most prominent ridge being situated ventro-medially on the valve and extending from posterior margin to anterior margin. A second lateral ridge just above also extends down to the anterior margin, but cannot be traced backwards beyond the anterior third where it dies out. Two short ridges branch off the ventro-median ridge a short distance back from the anterior margin. The uppermost ridge is very short and extends into valve centre at an acute angle whilst the lower extends below the ventro-median ridge, parallel to it for almost three-quarters of its length. Three short lateral ridges are situated in the dorso-median part of the posterior third. A short ridge extends down from the eye swelling to die out above mid-length. Ventro-median part of carapace convex, extended below ventral surface. On this extension the left valve has a single ridge extending almost from the anterior margin to the posterior margin, with a short lateral ridge below it in the anterior part of the valve. In the right valve there are two lateral ridges in this region, both convex ventrally. The upper extends the length of the posterior half of the valve whilst the ridge slightly offset below it extends the length of the anterior half with some overlap of the two at valve middle. Normal pore canals prominent. Hinge antimerodont. Left valve larger than right.

LECTOTYPE. I.1863, female carapace, figured Jones & Sherborn (1888), Blue Fuller's Earth Clay, Midford.

PARALECTOTYPES. I.1847, female right valve, figured Jones & Sherborn (1888), Blue Fuller's Earth Clay, Midford. Io.3642–45, two male and one female right valve from the Blue Fuller's Earth Clay and one female right valve from the Yellow Fuller's Earth Clay, Midford, Winwood Collection.

DESCRIPTION. Carapace with a strong posterior taper in both dimorphs, of which the male is the more elongate. Anterior end high, broadly rounded, the greatest height being through the anterior cardinal angle, just below which is a low eye swelling. Posterior end triangular, narrow, with concave postero-dorsal slope and convex postero-ventral slope. Posterior cardinal angle prominent. Greatest length passes through the mid-point, greatest width in the posterior third although the width in the anterior third is almost the same. Carapace constricted slightly about centre when viewed dorsally. Normal pore canals large and prominently displayed over the carapace. Shell surface ornamented as in the diagnosis. Left valve larger than the right, which it overlaps along the ventral margin and overreaches along the dorsal margin. **Hinge** antimerodont, only seen in the right valve where there are four to five terminal teeth and a rather long, delicate, loculate median groove. The hinge is particularly delicate, and the carapace as a whole appears to be thin-shelled. Inner margin and line of concrescence coincide. **Radial pore canals** and **muscle scars** not observed. A narrow flange extends around the anterior and ventral margins and along the ventral part of the posterior.

DIMENSIONS. I.1863, female carapace, length 0·57 mm.; height 0·31 mm.; width 0·25 mm. I.1847, female right valve, length 0·54 mm. (broken); height 0·32 mm. Io.3643, male right valve, length 0·65 mm.; height 0·33 mm. Io.3644, female right valve, length 0·58 mm.; height 0·33 mm. Io.3645, female right valve, length 0·56 mm.; height 0·31 mm.

REMARKS. The carapace morphology and surface ornamentation agree closely with the basic characters of those ostracods which may be placed in the *bradiana* grouping of *Lophocythere*. Apart from the details of the radial pore canals and muscle scars, which are not so far known for *L. acutiplicata*, the only character in disagreement with this classification is the hinge, which, being antimerodont, is at once at variance with all the other species of *Lophocythere*. An antimerodont hinge is normally accepted as present in juvenile instars of adults having an entomodont hinge; here the delicate shell, strong posterior taper and comparatively small size would indicate this if it were not for the presence of strong dimorphism suggesting adult status. Sexual dimorphism is known, however, in pre-adult instars. As only right valves are available for the examination of internal features, it is not intended to suggest a subgeneric rank for this species, until additional material becomes available. In ornamentation *L. acutiplicata* may be distinguished easily by the number of lateral ridges, their tendency to fade out in the posterior part of the carapace, and by the development of two ventro-lateral keels in the right valve.

Lophocythere bradiana (Jones)

(Pl. 4, figs. 2, 3; Text-fig. 4)

REMARKS. The species has already been described (p. 390).

DIMENSIONS. I.1854 (lectotype of *C. craticula* figured Jones & Sherborn, pl. 4, figs. 10*a–c*), length 0·62 mm.; height 0·32 mm.; width 0·32 mm. I.1867 (paralectotype of *C. craticula* figured Jones & Sherborn, pl. 4, figs. 9*a–c*) left valve, length 0·60 mm.; height 0·32 mm.

Lophocythere septicostata Bate

(Pl. 12, fig. 8)

1888 *Cytheridea bradiana* Jones & Sherborn : 272, pl. 4, figs. 11*a–c*.
1967 *Lophocythere septicostata* Bate : 52, pl. 15, figs. 7–13, pl. 16, figs. 1–4.

DIAGNOSIS. *Lophocythere* having seven longitudinal ridges on lateral surface and two on ventral surface. Vertical ridge extends downwards from oval eye swelling Interspaces between ridges punctate, with large, circular, normal pore canal openings. Anterior and posterior marginal borders compressed.

REMARKS. For remarks relating to this species see Bate (1967).

DIMENSIONS. I.1843, female right valve, length 0·64 mm.; height 0·33 mm.

Lophocythere sp.

(Text-fig. 12)

REMARKS. A single left valve in the Winwood Collection represents a new species of *Lophocythere*. It comes from the Blue Fuller's Earth Clay of Midford and is of the Bradiana Group. The arrangement of the lateral ridges is quite different from that in any described species. The dorsal ridge commences at the anterior margin, bends sharply upwards to pass through the eye swelling and then in an undulating

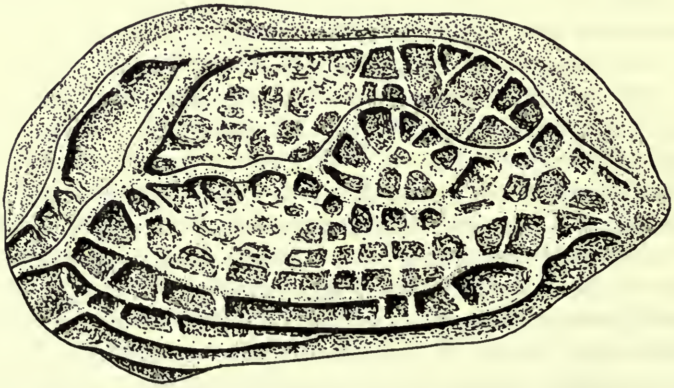


FIG. 12. *Lophocythere* sp. External view, right valve. Io.3900. × 170.

course parallels the dorsal and postero-dorsal margins to die out at the extreme posterior. The median ridge commences at the anterior margin just below the dorsal ridge and soon bifurcates, the ventral branch extending back into the posterior third. A second ridge branches from the median ridge a short distance above the first bifurcation and extends into the posterior third where it unites with the first bifurcation. Both then extend to the posterior margin as a single narrow ridge. The median ridge continues its dorsal course and bifurcates yet again, the dorsal branch continuing until it fuses with the dorsal ridge just behind the eye swelling; the other branch passes laterally back into the posterior half of the valve, splits into a reticulate complex of smaller ridges but re-forms to fuse with the dorsal ridge in the posterior quarter. Two ventral ridges originate at the anterior margin, the lower extending back into the posterior half of the valve whilst the upper is restricted to the anterior half only. Interspaces between the ridges are reticulate. Hinge strongly entomodont.

DIMENSIONS. Io.3900, left valve, length 0·50 mm.; height 0·27 mm.

OSTREATA GROUP

Lophocythere fulgurata (Jones & Sherborn)

(Pl. 12, fig. 7)

1888 *Cytheridea fulgurata* Jones & Sherborn : 273, pl. 4, figs. 12*a–c*.

DIAGNOSIS. Carapace sub-rectangular, tapering to the posterior. Oval, clear eye swelling at anterior cardinal angle. Anterior and posterior marginal areas flattened, smooth. Central part of carapace strongly convex, ornamented by two prominent ridges. The first, L-shaped, commences at the eye swelling, extends vertically down to the antero-ventral part of the valve, where it performs a right-angle, and runs laterally backwards to the edge of the posterior marginal area. A second lateral ridge arises just below the right-angled bend of the first ridge and extends backwards, paralleling the ridge above it, to die out in a similar position at the edge of the posterior marginal border. The area inside the " L " of the first ridge is occupied by strong ridges radiating down from the dorsal margin and occasionally branching.

LECTOTYPE. I.1832, right valve, figured Jones & Sherborn (1888), Blue Fuller's Earth Clay, Midford.

PARALECTOTYPES. Io.3646–8, right and left valves from the Blue Fuller's Earth Clay, Midford, Winwood Collection.

DESCRIPTION. Carapace sub-rectangular with dorsal margin sloping to posterior. Cardinal angles prominent, situated close to the anterior and posterior margins respectively. Anterior cardinal angle smooth, indicating the presence of an eye swelling. Line of greatest height passes through this point. Line of greatest length passes through the mid-point, or slightly below it. Anterior end high, broadly rounded; posterior end small and triangular with a concave postero-dorsal slope and a convex postero-ventral slope. Ventral margin with a shallow antero-median incurvature. Shell surface ornamented as in the diagnosis; area between the ridges appears to be punctate. Hinge not well preserved, the median element in both valves having been damaged. Terminal elements consist of dentate ridges in the right valve and loculate sockets in the left. Median bar of the left valve, long, not clearly seen to be dentate, bounded above by a shallow accommodation groove. Median groove of the right valve, long and narrow, not seen to be loculate because of damage. Inner margin and line of concrescence coincide. **Radial pore canals** and **muscle scars** not seen. A narrow flange extends around the anterior margin and along the ventral margin to the tip of the posterior margin in the right valve.

DIMENSIONS. I.1832, right valve, length 0·77 mm.; height 0·42 mm. Io.3648, left valve, length 0·66 mm.; height 0·36 mm.

REMARKS. Although the median element of the hinge has been damaged, the appearance suggests that it was antimerodont instead of the entomodont hinge typical of the genus. The strongly tapering outline and the hinge suggest that the material is of a pre-adult instar, but it is doubtful whether the adult ornamentation would be different from that described above. Certainly there is no difference between the instars examined.

Lophocythere ostreata (Jones & Sherborn)

(Pl. 12, fig. 5; Text-fig. 13)

1888 *Cytheridea ostreata* Jones & Sherborn : 271, pl. 4, figs. 6*a–c*.
1888 *Cytheridea bicarinata* Jones & Sherborn : 270, pl. 4, figs. 5*a–c*.
1948 *Lophocythere ostreata* (Jones & Sherborn) Sylvester-Bradley : 195, pl. 14, figs. 1–4, pl. 15, figs. 1, 2.
1963 *Lophocythere ostreata* (Jones & Sherborn); Oertli : 42, pl. 28, fig. 0, pl. 29, fig. 0.

DIAGNOSIS. Species of *Lophocythere* with characteristic L-shaped ridge commencing at a large, clear eye node, extending down to the antero-ventral region, to bend back at a right-angle and extend to the edge of the posterior marginal border. Second, keel-like ridge starts below the previous ridge in the antero-ventral part of the valve and extends backwards, parallel to the first ridge to die out against the edge of the posterior marginal border. Shell surface coarsely reticulate, the reticulations strongly upstanding to produce an oblique row of three prominent areas, the first of which is antero-central in position, just inside the angle of the L-shaped ridge. The second is dorso-median in position, just behind mid-point, whilst the third is postero-dorsal in position. Two, sometimes three, minor raised reticulations may be situated below and behind the two most dorsal of the major raised areas. Ventral surface with minor longitudinal ridges.

HOLOTYPE. I.1833, right valve figured Jones & Sherborn (1888), Yellow Fuller's Earth Clay, Midford.

Other material. Io.3945-7, two carapaces and two broken right valve fragments, Winwood Collection, Blue Fuller's Earth Clay, Midford. These were referred to by Jones & Sherborn (1888) and are syntypes of *Cytheridea bicarinata*, the figured specimen having been lost. Io.3945 is here selected lectotype of *C. bicarinata*.

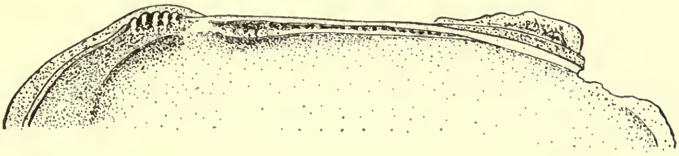


Fig. 13. *Lophocythere ostreata* (Jones & Sherborn). Internal view, right valve. Holotype, I.1833. × 105.

Description. Carapace sub-rectangular with sub-parallel dorsal and ventral margins in the adult. Juvenile specimens have distinct posterior taper. Anterior end high, broadly rounded, posterior end triangular, with concave postero-dorsal slope and convex postero-ventral slope. Cardinal angles prominent, rounded. Anterior cardinal angle with well-developed, oval, clear eye node situated just below. Line of greatest length passes through the mid-point, line of greatest height through anterior cardinal angle and of greatest width through the posterior third of the carapace. Ornamentation as in the diagnosis. The reticulations continue into the lateral ridges and pass on to the anterior and posterior marginal borders. The postero-dorsal raised area is not developed in juvenile instars. Left valve larger than the right, which it overlaps along the ventral margin but overreaches around the anterior and posterior margins and in the region of the cardinal angles. **Hinge** weakly entomodont, seen only in the right valve: anterior dentate ridge with six teeth, posterior element not seen, median groove poorly preserved and not definitely seen to be loculate, expanded slightly in the anterior half. Inner margin and line of concrescence coincide to produce a broad duplicature. Selvage distinct, flange developed around the anterior margin, extending from the anterior cardinal angle, along the ventral margin to the tip of the posterior margin. **Radial pore canals** and **muscle scars** not observed.

Dimensions. I.1833, right valve, length 0·81 mm.; height 0·40 mm. Io.3945, carapace, length 0·85 mm.; height 0·43 mm.; width 0·42 mm. Io.3947, juvenile carapace, length 0·60 mm.; height 0·31 mm.; width 0·28 mm.

Remarks. The Ostreata Group of *Lophocythere* is characterized by the presence of two lateral keel-like ridges, the upper of which turns upwards to produce a reverse L-shaped ridge. The ornamentation within this " L " varies according to the species. In *L. ostreata* the reticulate ornamentation, extended into a number of upstanding areas, is quite unlike any described species. Exaggerations in the ornamentation of species within this group tend to be in the same position as the areas emphasized in *L. ostreata*. In this connection the closest species is *L. scabra* Triebel (1951), although it does not possess the strong reticulate ornamentation of *ostreata*.

Genus *MICROPNEUMATOCYTHERE* Bate 1963

Micropneumatocythere limaciformis (Jones & Sherborn)

(Pl. 13, fig. 1)

1888 *Cytheridea limaciformis* Jones & Sherborn : 269 pl. 3 figs. 12*a–c*.

Diagnosis. Carapace oval/elongate with dorso-median area swollen, convex. projecting above dorsal margin in right valve; left valve with convex dorsal margin. Ventro-lateral and median part of ventral surface swollen, strongly convex, sometimes with weak longitudinal striae on ventral surface of convexity. Shell surface punctate. Normal pore canal openings large, circular, evenly spaced over the carapace.

Holotype. I.1831, male right valve, figured Jones & Sherborn (1888), Blue Fuller's Earth Clay, Midford.

Other material. Io.276 and 4007, and Io.3944, female right and left valves from the Bradford Clay, Bradford-on-Avon, and male right valve from the Blue Fuller's Earth Clay, Midford. Winwood Collection.

Description. Carapace oval/elongate in outline, the more elongate specimens being the males. In the right valve of both dimorphs, especially the male, the dorso-median part of the valve is distinctly swollen, the convex surface projecting above the dorsal margin. Similarly the ventro-lateral part of the valve is also swollen but involves the ventral surface where, in some specimens, weak longitudinal striae are present. Left valve with uniformly convex dorsal and ventral margins. Anterior end uniformly rounded, posterior end triangular with concave postero-dorsal slope and convex postero-ventral slope, the posterior extremity tending to be upturned. Cardinal angles particularly distinct in the right valve, apparently separated from the central convexity of the valve by a shallow groove. Greatest length of carapace passes through the mid-point with the greatest height and width also at valve centre. Shell surface finely punctate with prominent, large, circular normal pore canal openings evenly spaced over the carapace. **Hinge** almost certainly antimerodont, the terminal dentate/loculate elements being clearly seen, whilst the median bar and groove is not sufficiently well preserved to state that it is a dentate/loculate structure. Inner margin and line of concrescence coincide, anterior **radial pore canals** straight, evenly spaced around the anterior margin, exact number not observed but no more than eight. A narrow flange extends around the anterior margin of the right valve and along the median part of the ventral margin. **Muscle scars** not seen.

Dimensions. I.1831, male right valve, length 0·71 mm.; height 0·37 mm. Io.3944, male right valve, length 0·62 mm.; height 0·32 mm. Io.276, female right valve, length 0·56 mm.; height 0·36 mm. Io.4007, female left valve, length (damaged) 0·61 mm.; height 0·37 mm.

Remarks. The closest species is *M. quadrata* Bate (1967), particularly in the case of the male dimorph. However, the characteristic development of a deep postero-ventral slope in *M. quadrata* and the less strongly developed dorso-median convexity of the right valve distinguish this species from *M. limaciformis*.

Genus ***PROGONOCYTHERE*** Sylvester-Bradley 1948

Progonocythere stilla Sylvester-Bradley

(Pl. 13, fig. 2)

1948 *Progonocythere stilla* Sylvester-Bradley : 190, pl. 12, figs. 1, 2, pl. 13, figs. 1, 2.
1956 *Progonocythere stilla* Sylvester-Bradley; Grekoff : pl. 13, figs. 325–7.
1963 *Progonocythere stilla* Sylvester-Bradley; Oertli : 44, pl. 28, fig. *n*, pl. 29, fig. *n*.

DIAGNOSIS. *Progonocythere* with finely punctate shell surface, large, circular normal pore canal openings, somewhat irregularly scattered, tending to be concentrated towards centre of valve. Anterior end high, broadly rounded. Anterior cardinal angle close to anterior margin. Cardinal angles well rounded in left valve more distinctly angled in right. Dorsal margin convex in right valve, straight in left, in both valves steeply sloping to posterior. Posterior rounded in left valve, slightly angled in right. Anterior marginal border distinct from convexity of valve, ventrolateral margin strongly convex, overhanging ventral margin. Left valve larger than the right. Hinge entomodont. Other internal features as for genus. Dimorphic.

REMARKS. *Progonocythere stilla*, the type species of the genus, was described by Sylvester-Bradley from the Bathonian Boueti Bed of Langton Herring. A single left valve (Io.3657) found in the Winwood Collection, from the Blue Fuller's Earth Clay of Midford, was not described by Jones & Sherborn. Three specimens (Io.3584–6) in the Möckler Collection are from the Fuller's Earth of Midford.

DIMENSIONS. Io.3657, left valve, length 0·60 mm.; height 0·43 mm.

Genus ***TERQUEMULA*** Blaszyk & Malz 1965

Terquemula blakeana (Jones)

(Pl. 4, fig. 8)

REMARKS. For synonymy and diagnosis see p. 393. The two specimens in the Jones & Sherborn Collection which have been placed in the synonymy are: *Cytheridea transversiplicata*, figured Jones & Sherborn 1888, pl. 3, figs. 4*a–c*, I.1828 (holotype), right valve, length 0·59 mm.; height 0·31 mm., and *Cytheridea blakeana* (Jones) Jones & Sherborn, figured pl. 2, figs. 11*a–c*. I.1853, left valve, length 0·60 mm.; height 0·31 mm. In addition a single right valve, Io.3941, has been found in the Winwood Collection from the Blue Fuller's Earth Clay, Midford.

INCERTAE SEDIS

The following ostracod species described by Jones & Sherborn are represented by single specimens only. They are retained here under their original names until comparative material enables a more precise determination.

" *Cythere* " *corrosa* Jones & Sherborn

(Pl. 13, fig. 4)

1888 *Cythere corrosa* Jones & Sherborn : 254, pl. 2, figs. 12*a–c*.

HOLOTYPE. I.1865, figured Jones & Sherborn (1888), Blue Fuller's Earth Clay, Midford.

REMARKS. This small ostracod resembles *Caytonidea* in outline and reticulate ornamentation, but differs in possessing a well-defined anterior marginal border. In *Caytonidea* the convex outline of the carapace continues without a break on to the anterior margin. Internal features not seen.

DIMENSIONS. I.1865, carapace, length 0·49 mm.; height 0·28 mm.; width 0·28 mm.

" *Cytheridea* " *aequabilis* Jones & Sherborn

(Pl. 13, fig. 3)

1888 *Cytheridea aequabilis* Jones & Sherborn : 257, pl. 1, figs. 1*a–c*.

HOLOTYPE. I.1864, figured Jones & Sherborn (1888), Yellow Fuller's Earth Clay, Midford.

REMARKS. *C. aequabilis* has a finely punctate carapace, rounded anterior and posterior margins, and parallel dorsal and ventral margins. In outline it is close to the unidentified ostracod figured by Bate (1964, pl. 13, figs. 5–8). Internal features not seen.

DIMENSIONS. I.1864, carapace, length 0·71 mm.; height 0·30 mm ; width 0·32 mm.

" *Cytheridea* " *coarctata* Jones & Sherborn

(Pl. 13, fig. 5)

1888 *Cytheridea coarctata* Jones & Sherborn : 259, pl. 1, figs. 3*a–c*.

HOLOTYPE. I.1841, figured Jones & Sherborn (1888), Blue Fuller's Earth Clay, Midford.

REMARKS. The unornamented carapace, well-rounded anterior and posterior margins, parallel dorsal and ventral margins, together with a muscle scar pattern in which the antero-dorsal antennal scar is crescentic in shape (type **B**), suggest *Homocytheridea* Bate (1963*a*). The left valve, the only known specimen, has been broken posteriorly and a more definite identification is not attempted.

DIMENSIONS. I.1841, left valve, length (broken) 0·56 mm.; height 0·26 mm.

" *Cytheridea* " *eminula* Jones & Sherborn

(Pl. 13, fig. 6)

1888 *Cytheridea eminula* Jones & Sherborn : 261, pl. 1, figs. 11*a–c*.

LECTOTYPE. I.1839, figured Jones & Sherborn (1888), Blue Fuller's Earth Clay, Midford.

REMARKS. This species is represented by a single left valve, although two specimens were included in the original description.

DIMENSIONS. I.1839, left valve, length 0·54 mm.; height 0·31 mm.

" *Cytheridea* " *punctiputeolata* Jones and Sherborn

(Pl. 13, fig. 8)

1888 *Cytheridea punctiputeolata* Jones & Sherborn : 258, pl. 1, figs. 4*a–c*.

HOLOTYPE. I.1856, figured Jones & Sherborn (1888), Blue Fuller's Earth Clay, Midford.

REMARKS. Although at first appearing to resemble the male dimorph of *Hadrocytheridea dolabra* the present species differs in the much more rounded posterior margin, in the greater exaggeration of the ornamentation, which here consists of large, circular pits with the interspaces between distinctly punctate, and in the lophodont hinge.

DIMENSIONS. I.1856, right valve, length 0·73 mm.; height 0·32 mm.

" *Cytheridea* " *retorrida* Jones & Sherborn

(Pl. 15, fig. 3; Text-figs. 14, 15)

1888 *Cytheridea retorrida* Jones & Sherborn : 260, pl. 1, figs. 8*a–c*.

MATERIAL. Io.3923, Blue Fuller's Earth Clay, Midford. Winwood Collection.

REMARKS. The figured specimen was never presented and is presumed lost. A single carapace of this species has been found in the Winwood Collection, but

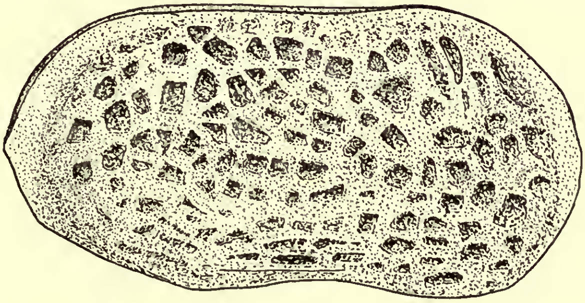


FIG. 14. *Cytheridea retorrida* Jones & Sherborn. Right valve, complete carapace. Io.3923. × 135.

cannot be assigned to a known genus. Like *C. corrosa* it has some affinities with *Caytonidea* but has been excluded on the presence of distinct marginal borders. No internal features are known.

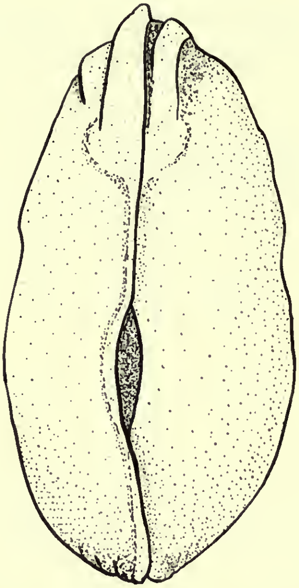


FIG. 15. *Cytheridea retorrida* Jones & Sherborn. Dorsal view of carapace with ornamentation omitted. Io.3923. × 135.

DIMENSIONS. Io.3923, carapace, length 0·54 mm.; height 0·28 mm.; width 0·28 mm.

" *Cytheridea* " *spinifastigiata* Jones & Sherborn

(Pl. 13, fig. 7)

1888 *Cytheridea spinifastigiata* Jones & Sherborn : 264, pl. 2, figs. 8*a–c*.

HOLOTYPE. I.1861, figured Jones & Sherborn (1888), Blue Fuller's Earth Clay, Midford.

REMARKS. It is not possible to assign the single left valve to any known genus.

DIMENSIONS. I.1861, left valve, length 0·60 mm.; height 0·33 mm.

" *Cytheridea* " *spinigyrata* Jones & Sherborn

(Pl. 13, fig. 9)

1888 *Cytheridea spinigyrata* Jones & Sherborn : 264, pl. 2, figs. 7*a–c*.

HOLOTYPE. I.1860, figured Jones & Sherborn (1888), Blue Fuller's Earth Clay, Midford.

REMARKS. Jones & Sherborn (p. 264) compared this species with *Cythere drupacea* Jones but at the same time pointed out differences. The superficial similarity of *C. spinigyrata* to *C. drupacaea* suggests that it, too, might belong to *Metacytheropteron* Oertli (1957).

DIMENSIONS. I.1860, right valve, length 0·61 mm.; height 0·34 mm.

IV. THE J. F. BLAKE COLLECTION

Order MYODOCOPIDA Sars 1866

Suborder CLADOCOPINA Sars 1866

Family **POLYCOPIDAE** Sars 1866

Genus ***POLYCOPE*** Sars 1866

Polycope fungosa sp. nov.

(Pl. 16, figs. 4, 9)

DIAGNOSIS. Carapace oval in adults, almost circular in juvenile instars. Shell surface strongly pitted with weak striae near and parallel to the free margin. Anterior end flattened, with marginal denticles. Hinge short, sunk in dorsal groove. Anterior cardinal angle prominent, antero-dorsal slope long, broadly convex with prominent overlap of left valve by the right. Posterior end broadly rounded, ventral margin strongly convex. Carapace distinctly angled at junction of antero-dorsal slope and anterior margin. Right valve larger than left.

HOLOTYPE. Io.3951, carapace, Fuller's Earth, Midford, near Bath.

PARATYPES. Io.3952–5, one adult and eighteen juvenile carapaces. Horizon and locality as above.

DESCRIPTION. Carapace in adult specimens oval in outline, laterally compressed. Lines of greatest length and height pass through the mid-point. Greatest width in the holotype situated at the extreme posterior end. A shallow central depression on the lateral surface marks the position of the muscle scars. Hinge margin situated in the posterior half of the carapace and sunk into a dorsal groove, at the anterior end of which the cardinal angle is prominently developed. Antero-dorsal slope long and convex, terminating in a sharply angled junction with the obliquely flattened anterior end. Posterior end broadly rounded, ventral margin broadly convex. Shell surface uniformly and distinctly pitted; striae are developed in the anterior and ventro-lateral regions. In dorsal view one stria on each valve can be seen to project beyond the anterior margin. Striations are arranged parallel to the free margins. Anterior margin may develop small denticles, though these, like the surface ornamentation, are generally absent from the juvenile instars. Right valve larger than the left, which it overlaps strongly along the antero-dorsal slope and less strongly around the posterior end. Internal features not observed.

DIMENSIONS. Io.3951, carapace, length 0·54 mm.; height 0·44 mm.; width 0·23 mm. Io.3952, carapace, length 0·46 mm.; height 0·37 mm.; width 0·20 mm.

Io.3953, juvenile carapace, length 0·32 mm.; height 0·27 mm.; width 0·09 mm. Io.3954, juvenile carapace, length 0·26 mm.; height 0·22 mm.; width 0·01 mm.

Remarks. A number of species of *Polycope* have been described from the Lower Jurassic (Apostolescu 1959; Fischer 1961 and Blake 1876), Middle Jurassic (Terquem 1885) and Upper Jurassic (Donze 1962 and Oertli 1959). *P. fungosa* differs from them all in the type of ornamentation present. A number of specimens in the Blake collection labelled *Polycope* sp. are probably juvenile specimens of the present species but lack the specific ornamentation.

Family **PROGONOCYTHERIDAE** Sylvester-Bradley 1948

Genus ***TRACHYCYTHERE*** Triebel & Klingler 1959

Remarks. *Trachycythere* Triebel & Klingler (1959 : 343), first described from the Lias of Germany and later recorded from the Upper Bathonian of France (Oertli 1963), was placed in the Family Trachyleberididae (Moore 1961 : 341). Later Bate (1967*a* : 551) transferred it to the Progonocytheridae, a classification retained in this paper.

Trachycythere sp.

(Pl. 16, fig. 3)

Remarks. A single left valve represents this Upper Bathonian species, which differs in being sub-rectangular with almost parallel dorsal and ventral margins, from two of the three species originally described by Triebel & Klingler, which have a more pronounced posterior taper. *Trachycythere verrucosa* Triebel & Klingler (1959) resembles this species in outline, but has stronger, more massive tubercles.

Dimensions. Io.3966, left valve, length 0·45 mm.; height 0·25 mm.

Genus ***HEKISTOCYTHERE*** nov.

Derivation of name. *Hekistos* (Gr.), least, + *cythere*.

Diagnosis. A small genus with oval, posteriorly tapering carapace. Greatest height close to the anterior margin. Left valve larger than right. Hinge lophodont. Muscle scars of type **A** although antennal scar tends to be almost centrally situated in front of adductors. Radial pore canals straight, widely spaced, ten anteriorly, four posteriorly. Duplicature narrow.

Type species. *Hekistocythere venosa* sp. nov.

Hekistocythere venosa gen. et sp. nov.

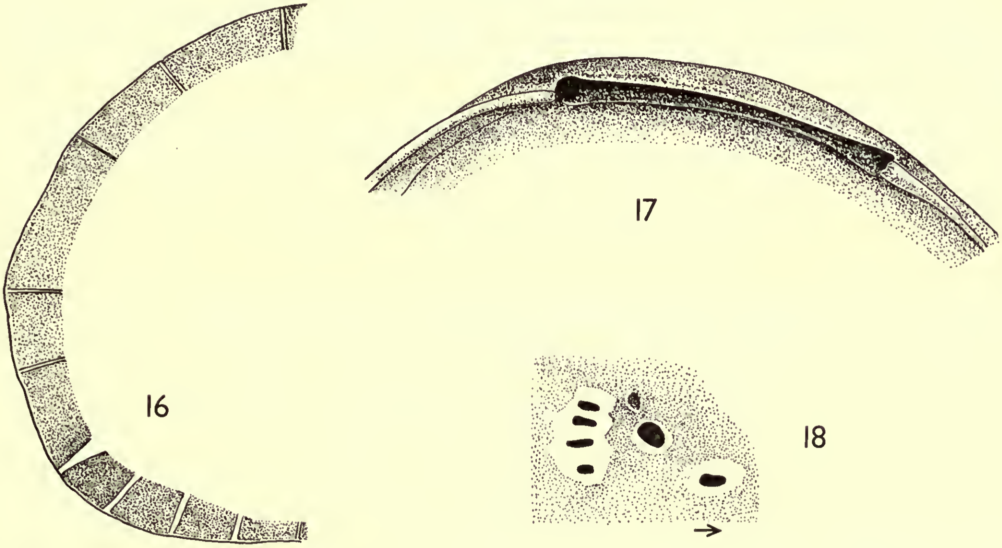
(Pl. 14, figs. 2, 4, 9; Pl. 15, fig. 7; Text-figs. 16–18)

Diagnosis. *Hekistocythere* with strongly ornamented carapace. Broad diagonal ridge extends from postero-dorsal to antero-ventral region of valve. Short, thick, subsidiary ridges given off on dorsal and ventral sides of main ridge. Smaller intermediary ridges producing a reticulate ornamentation. Diagonal ridge produced at termination of, and at right-angles to, main ridge in postero-dorsal region.

Holotype. Io.3995, carapace, Fuller's Earth, Bath.

Paratypes. Io.3996–9 (seven specimens) and Io.4011–3, Fuller's Earth, Bath.

Description. Carapace small with high, rounded anterior end and narrow, rounded posterior end. Carapace parallel-sided in dorsal view. Line of greatest length passes through the mid-point. Greatest width in either the anterior or posterior third, the carapace being slightly constricted medially. Dorsal margin convex, especially in the right valve where it projects slightly above that of the left valve. Surface ornamentation very coarsely reticulate, produced by a series of irregular ridges, the major of which extends down from the postero-dorsal part of the valve and extends to the antero-ventral region. From this ridge a number of irregular and shorter ridges branch off on its dorsal and ventral sides. One of the secondary ridges is particularly noticeable in dorsal view, and this leaves the primary ridge in the posterior part of the valve to extend dorsally in an antero-dorsal direction until it fuses with the dorsal margin. Left valve larger than the right, which it overlaps along the ventral margin and overreaches in the region of the antero- and



Figs. 16–18. *Hekistocythere venosa* sp. nov. Fig. 16. Anterior radial pore canals. Paratype, Io.4013. × 300. Fig. 17. Hinge, right valve, paratype, Io.4011. × 300. Fig. 18. Muscle scars, left valve, paratype, Io.3997. × 300.

postero-dorsal slopes. Ventral surface flattened, triangular in outline, widening towards the posterior end. **Hinge** lophodont: right valve with smooth terminal elements which are the dorsal terminations of the selvage; median groove deeply recessed, smooth. Left valve with smooth terminal sockets open ventrally to the interior of the valve. Median bar long, smooth, convex, the convexity of the bar facing upwards. Inner margin and line of concrescence coincide, the duplicature being rather narrow. **Radial pore canals** short and straight and widely spaced, ten anteriorly and four posteriorly. **Muscle scars** of type **A** (Bate 1963), with four adductor scars in a slightly crescentic row; the second dorsal adductor is laterally elongate with the rounded antennal scar situated in front.

Dimensions. Io.3995, carapace, length 0·32 mm.; height 0·20 mm.; width 0·15 mm. Io.3996, left valve, length 0·32 mm.; height 0·21 mm. Io.4011, right valve, length 0·32 mm.; height 0·20 mm. Io.4012, left valve, length 0·33 mm.; height 0·21 mm.

Remarks. *Hekistocythere* has a distinctive combination of lophodont hinge, small, oval, posteriorly tapered carapace, type **A** muscle scars, and simple radial pore canals.

Family **PROTOCYTHERIDAE** Ljubimova 1955

Subfamily **KIRTONELLINAE** Bate 1963

Genus ***EKTYPHOCYTHERE*** Bate 1963

Ektyphocythere parva (Oertli)

(Pl. 14, figs. 1, 3)

1959 *Procytheridea minuta* Oertli : 122, pl. 3, figs. 37–40.
1960 *Procytheridea parva* Oertli : 70.

Remarks. Two complete carapaces represent this species, one male the other female.

When first erected, *Ektyphocythere* Bate (1963) included those species of "*Procytheridea*" which possessed, amongst other characters, a triangular arrangement of ridges as ornamentation and an antimerodont hinge. *P. parva* was one of the species included.

Subsequently Malz (1966) placed *Ektyphocythere* in synonymy with *Kinkelinella* Martin (1960) the type species, *K. tenuicostati* Martin (1960), having a reticulate ornamentation. Although considered here to be closely related the clear distinction between the forms having a triangular rather than a reticulate ornamentation is such that the retention of the former in *Ektyphocythere* is maintained here.

Dimensions. Io.3982, female carapace, length 0·41 mm.; height 0·23 mm.; width 0·21 mm. Io.3983, male carapace, length 0·45 mm.; height 0·23 mm.; width 0·24 mm.

FAMILY UNCERTAIN

Genus ***PLATYCYTHERE*** Bate 1967

Platycythere sp.

(Pl. 14, fig. 5)

REMARKS. Represented by a single specimen only. In outline and possession of dorsal and ventro-lateral swellings this species exhibits the generic features described (Bate 1967), but differs from *Platycythere verriculata*, the type species, by having a much finer reticulate ornamentation and a median swelling on the lateral surface of both valves. This swelling, positioned about the centre of the valve, has an oblique postero-dorsal antero-ventral inclination.

Gesoriacula Oertli (1959) has a similar external morphology but a more primitive hinge structure.

DIMENSIONS. Io.3992, carapace, length 0·35 mm.; height 0·20 mm.; width 0·16 mm.

Family **CYTHERURIDAE** Müller 1894

Genus ***LOONEYELLA*** Peck 1951

REMARKS. The type species, *Cythere monticula* Jones (1893), was described from the Cretaceous Bear River Formation, Cokeville, south-west Wyoming, in association with fresh- to brackish-water ostracods. Peck (1951), in resampling this Formation, found a new ostracod species which he considered to be congeneric with *C. monticula*, and for these two species erected the genus *Looneyella*, *C. monticula* being the type.

The preservation of Peck's material is considerably better than that of the holotype, which is in the Museum collections. The latter, I.5872, figured Jones (1893, pl. 15, fig. 13), is a complete carapace, length 0·65 mm.; height 0·40 mm.; width 0·39 mm. (inclusive of spines). The holotype is figured here (Pl. 14, fig. 6) for comparison with the Bathonian species *L. subtilis*.

To date the following species have been placed in *Looneyella*:

L. monticula (Jones) from the Upper Cretaceous Bear River Formation.
L. quadrispina Peck 1951, also from the Bear River Formation.
L. subtilis Oertli, from the Bathonian of the Boulonnais, France.

Looneyella subtilis Oertli

(Pl. 14, figs. 7, 8)

1959 *Looneyella ? subtilis* Oertli : 119, pl. 3, figs. 31–5.

DIAGNOSIS. Small species of *Looneyella* with prominent postero-dorsal tubercle, an antero-median tubercle somewhat smaller in size, and a marginal ridge which extends around the anterior margin and along the ventro-lateral alar extension. Both tubercles and marginal ridge are hollow when viewed internally. Antero-medially there is a break in the continuity of the marginal ridge. Small swelling may be present below the postero-dorsal tubercle, and at the termination of the alar ridge. Shell surface smooth except for ventral surface which has four longitudinal striae per valve. Left valve larger than right. Hinge antimerodont. Species dimorphic. Eight straight anterior radial pore canals; inner margin and line of concrescence coincide. Low eye swelling occurs at the anterior cardinal angle and is connected to the anterior marginal ridge.

REMARKS. Oertli placed this species only tentatively in *Looneyella*, but comparison with the holotype of the type species convinces me that *L. subtilis* is congeneric. Dr. Oertli kindly sent me specimens of his material for comparison and enabled me to examine internal characters not available in my material.

Ecologically this is an interesting genus with the Cretaceous species recorded from sediments considered to be non-marine whilst *L. subtilis* occurs in truly marine conditions. Possibly the Cretaceous species lived under brackish-water conditions.

The material from the Upper Bathonian Bradford Clay of Bradford consists of a single female carapace in the Winwood Collection (Io.3659), and two male carapaces and a juvenile carapace (Io.3956–8) from the Fuller's Earth of Bath in the Blake Collection.

DIMENSIONS. Io.3659, female carapace, length 0·37 mm.; height 0·22 mm.; width 0·21 mm. Io.3957, male carapace, length 0·35 mm.; height 0·18 mm.; width 0·17 mm.

Genus ***ORTHONOTACYTHERE*** Alexander 1933

Orthonotacythere sp.

(Pl. 15, fig. 1)

REMARKS. The single specimen is a small carapace having a high caudal process, a long, straight dorsal margin and a ventral surface triangular in outline. The lateral surface is weakly reticulate but prominently ornamented by three large tubercles. The first occurs at the anterior cardinal angle and is an eye tubercle. The second occurs at the postero-dorsal part of the carapace and is somewhat elongate in outline, whilst the third is situated directly below the second at the postero-ventral corner of the carapace. This last tubercle, positioned at the end of a somewhat thickened ventro-lateral margin, extends slightly beyond the carapace posteriorly. A weak lateral ridge is present at about valve centre, but does not estend as far as the terminal margins.

Orthonotacythere nodosa Plumhoff (1963), which appears in the Lias of Germany, differs from the present species in possessing a much larger number of tubercles. *?O. pulchella* Apostolescu (1959) from the Lias of France does not belong to this genus. *Orthonotacythere* sp. also differs from the small number of species described from the Upper Jurassic of the U.S.S.R. (Ljubimova 1955), Germany (Triebel 1941) and France (Donze 1960).

DIMENSIONS. Io.3993, carapace, length 0·30 mm.; height 0·15 mm.; width 0·14 mm.

Genus *PARARISCUS* Oertli 1959

Parariscus bathonicus Oertli

(Pl. 15, figs. 2, 8)

1959 *Parariscus bathonicus* Oertli : 118, pl. 2, figs. 20–29.

Remarks. Eight complete carapaces of this interesting species are present in the Blake Collection of Fuller's Earth Ostracoda. Dr. H. J. Oertli kindly sent me comparative material.

Dimensions. Io.3959, carapace, length 0·43 mm.; height 0·21 mm.; width 0·20 mm.

Genus *PARACYTHERIDEA* Müller 1894

Paracytheridea? blakei sp. nov.

(Pl. 15, figs. 4, 5, 9, 10)

Diagnosis. Carapace small, reticulate, with dorso-median constriction. Postero-ventral angle swollen, extended backwards beyond margin. Eye node developed at anterior cardinal angle. Dorsal margin long, straight. Anterior end high, rounded. Posterior end narrow, triangular, situated high on carapace.

Holotype. Io.4001, carapace, Fuller's Earth, Bath.

Paratypes. Io.4014–6, three carapaces, Fuller's Earth, Bath.

Description. Carapace small with coarse reticulate ornamentation. Dorso-median part of each valve with broad depression. Ventro-lateral margin swollen, particularly towards the posterior end where, at the postero-ventral angle, there is a backward projection of the carapace beyond the steeply angled postero-ventral slope. Dorsal margin long and straight with sharply angled cardinal angles. An **eye node** is situated behind the anterior cardinal angle. Anterior end high, rounded. Posterior end situated high on the carapace, sharply triangular with short, concave postero-dorsal slope and long, convex postero-ventral slope. Line of greatest length slightly above the mid-point; greatest height at the anterior cardinal angle. Greatest width in the posterior third. Left valve slightly larger than the right, which it overlaps along the ventral margin. Internal features not seen apart from the **muscle scars** which are visible from the exterior: these consist of a slightly crescentic row of four adductor scars, an antero-ventral, rounded, manibular scar, and an antero-dorsal antennal scar which is composed of two scars, the first crescentic in shape, the second rounded and fitting inside the crescent of the first. These muscle scars are situated low down on the carapace, below the dorso-median depression.

Dimensions. Io.4001, holotype, carapace, length 0·30 mm.; height 0·16 mm.; width 0·14 mm.

Remarks. *Paracytheridea? blakei* was named after J. F. Blake, in whose collection the species was found. A new genus might be preferred, but for the present it is sufficient to place the species in *Paracytheridea* on the basis of the external shape. There is no strong nodose ornamentation as in *Paracytheridea? caytonensis* Bate (1965).

Genus *CYTHERURA* Sars 1866

Cytherura bathonica sp. nov.

(Pl. 16, figs. 5–8)

DIAGNOSIS. *Cytherura* with small, elongate carapace, ornamented with slender, almost parallel, striae. Short, vertical connecting bars between striae present a slightly reticulate appearance. Posterior extremity situated above the line of the longitudinal axis.

HOLOTYPE. Io.4017, carapace, Fuller's Earth, Bath.

PARATYPES. Io.4018–9 and Io.4120, eight carapaces. Fuller's Earth, Bath.

DESCRIPTION. Carapace small, elongate, with line of greatest length very slightly above the mid-point. Greatest height at the extreme anterior end, greatest width in the posterior third. Shell surface ornamented by slender, almost parallel striae with connecting vertical bars between. A slightly reticulate appearance is thereby presented although this is subordinate to the sub-parallel striae. Dorsal and ventral margins long, straight and almost parallel. Anterior end broadly rounded, posterior end with narrow triangular margin terminally truncated and set high on the carapace: the concave postero-ventral slope is much longer than the concave postero-dorsal slope. Left valve only slightly larger than the right, overlapping it ventrally just anterior of median and at the cardinal angles. The right valve overlaps the left along the dorsal margin. Internal features not seen.

DIMENSIONS. Io.4017, carapace, length 0·30 mm.; height 0·13 mm.; width 0·10 mm. Io.4018, carapace, length 0·31 mm.; height 0·14 mm.; width 0·11 mm.

REMARKS. *Cytherura bathonica* is a true *Cytherura* as far as the external details are concerned. The presence of this species and *C. mediojurassica* sp. nov. in the Bathonian indicates that the genus was established by or during the Middle Jurassic. *C. bathonica* differs from previously described species in ornamentation although it comes close to the Recent *Cytherura striata* Sars (1866) from which it may be distinguished by the position of the posterior extremity, which is situated below the longitudinal axis in *C. striata* and above in *C. bathonica*.

Cytherura mediojurassica sp. nov.

(Pl. 15, fig. 6; Pl. 16, figs. 1, 2)

DIAGNOSIS. *Cytherura* with reticulate ornamentation. Carapace elongate, dorsal and ventral margins long, almost parallel but converging slightly towards posterior end. Short caudal process set high up on carapace.

HOLOTYPE. Io.4121, carapace, Fuller's Earth, Bath.

PARATYPES. Io.4122–38, sixteen carapaces, Fuller's Earth Clay, Bath.

DESCRIPTION. Carapace elongate with long, sub-parallel dorsal and ventral margins which converge slightly towards the posterior end. Greatest length of carapace through the mid-point whilst the greatest height is at the extreme anterior end, through the anterior cardinal angle. Greatest width in the posterior third. Carapace slender in dorsal view. Anterior end rounded, posterior end with short caudal process set high on the carapace, slightly above the line of greatest length. Postero-dorsal slope short, concave; postero-ventral slope long and concave, although in some specimens it is slightly convex. Termination of caudal process truncated. Shell surface ornamented by a rather coarse reticulation. Occasionally a weak longitudinal stria is present in the posterior half of the carapace and extends along the longitudinal axis as far as the valve centre. This striation is really an exaggerated development of the reticulation and in the holotype is present only on the right valve. Left valve slightly larger than the right in that it overlaps the right along the ventral margin, especially along its anterior half. Dorsally, however, the right valve overreaches the left. Internal features not known.

DIMENSIONS. Io.4121, carapace, length 0·33 mm.; height 0·15 mm.; width 0·13 mm. Io.4122, carapace, length 0·31 mm.; height 0·15 mm.; width 0·12 mm.

REMARKS. *Cytherura mediojurassica* sp. nov. is easily distinguished from *C. bathonica* by its strong reticulate ornamentation, and from *Cytherura? liesbergensis* Oertli (1959) by its more elongate carapace in which the dorsal and ventral margins are sub-parallel. In addition the ornamentation of *C.? liesbergensis* is weakly reticulate, with four lateral striae extending along most of the length of the carapace. These striae are not represented in the present species. Dr. H. J. Oertli kindly sent me comparative material.

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EXPLANATION OF PLATES

All the specimens illustrated are in the Department of Palaeontology, British Museum (Natural History). With the exception of Pl. 5, figs. 5, 6, and Pl. 16, fig 4, the photographs were taken by the author with the Stereoscan scanning electron microscope.

PLATE 1

FIG. 1. ***Cytherella symmetrica*** Jones. External view, male left valve and lectotype of *Cytherella subovata* Jones. IN.43496. × 75.

FIG. 2. ***Cytherella symmetrica*** Jones. External view of lectotype, female left valve. IN.43503. × 85.

FIG. 3. ***Cytherelloidea jugosa*** (Jones). External view of lectotype, female right valve. IN.43497. × 120.

FIG. 4. ***Cytherelloidea jugosa*** (Jones). External view of paralectotype, left side of female carapace. I.2311. × 115.

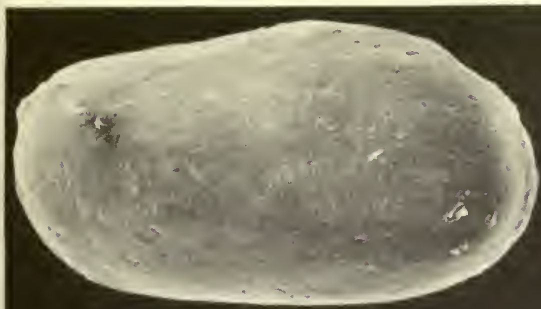
FIG. 5. ***Bairdia hilda*** Jones. Right valve of complete carapace, paralectotype, Io.3608. × 78.

FIG. 6. ***Bairdia hilda*** Jones. Left valve, lectotype, IN.41951. × 73.

FIG. 7. ***Bairdia juddiana*** Jones. Right valve of complete carapace, holotype, IN.43506. × 65.

FIG. 8. ***Lophocythere acutiplicata*** (Jones & Sherborn). Male right valve, paralectotype, Io.3643. × 95.

PLATE 1



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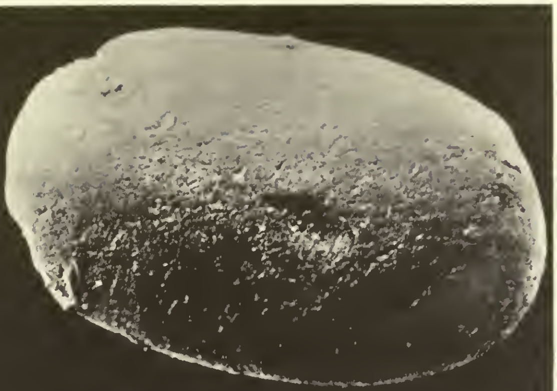

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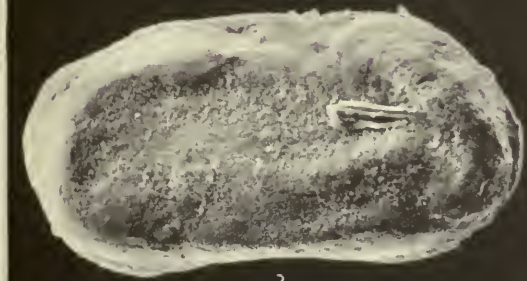

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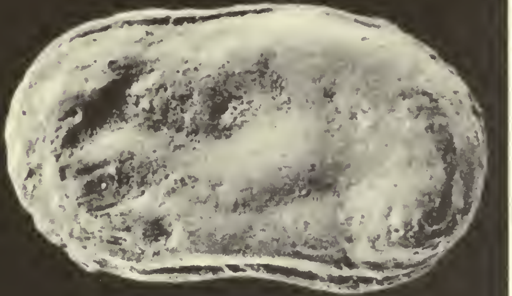

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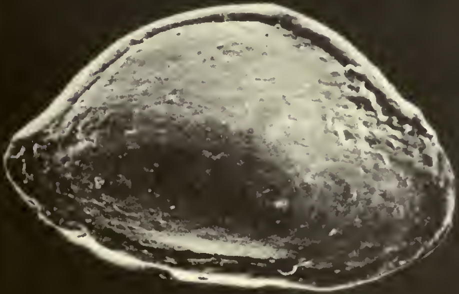

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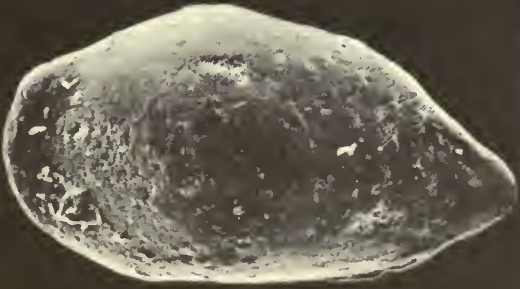

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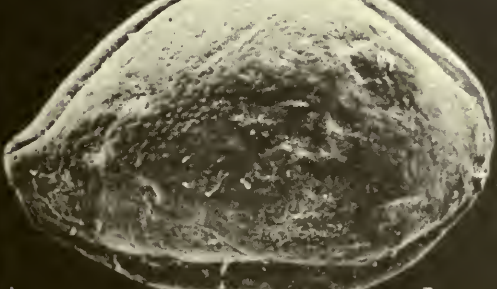

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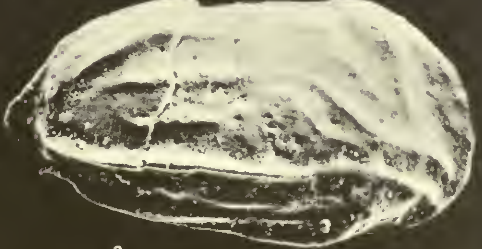

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PLATE 2

FIG. 1. **Bairdia jurassica** Jones. Left valve of complete carapace, lectotype, IN.43494. × 73.

FIG. 2. **Bairdia jurassica** Jones. Right valve of complete carapace, paralectotype. Specimen figured and described by Jones as *B. jurassica* var *tenuis*. IN.43495. × 73.

FIG. 3. **Pontocyprella harrisiana** (Jones). Left valve of specimen figured and described by Jones as *Macrocypris bradiana*. IN.43500. × 70.

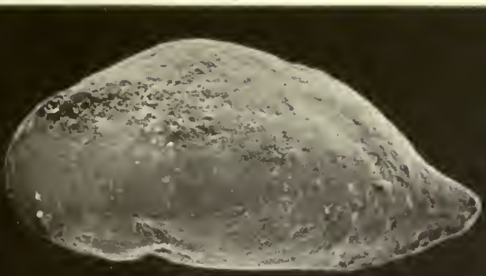
FIG. 4. **Schuleridea (Eoschuleridea) subperforata** (Jones). External view, right valve, lectotype, originally figured as *Cytheridea subperforata* (in part) by Jones. IN.43504. × 97.

FIG. 5. **Schuleridea (Schuleridea) jonesiana** (Bosquet). External view, left valve of complete carapace originally figured as *Cytheridea subperforata* (in part) by Jones. IN.43490. × 73.

FIG. 6. **Praeschuleridea schwageriana** (Jones). Right valve of complete carapace, holotype. IN.43499. Originally figured as *Cythere schwageriana* Jones. × 99.

FIG. 7. **Schuleridea (Eoschuleridea) trigonalis** (Jones). Right valve, complete carapace, holotype. IN.42373. Originally described as *Bairdia trigonalis* Jones. × 85.

FIG. 8. **Praeschuleridea** sp. Right valve of complete female carapace, Io.3619. × 98.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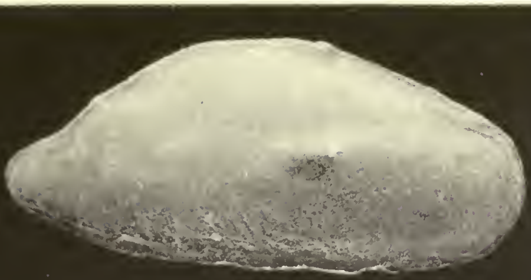
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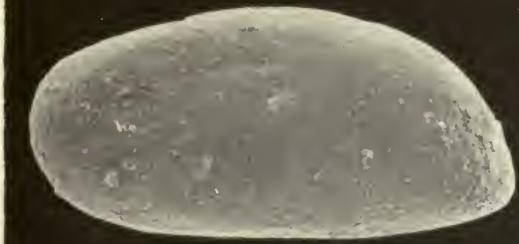
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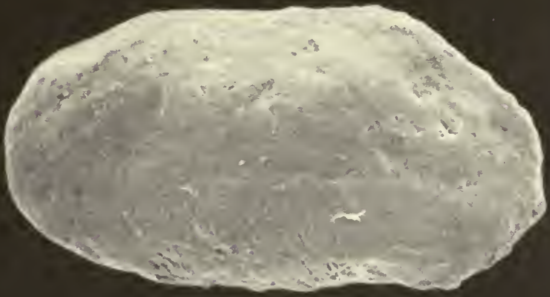
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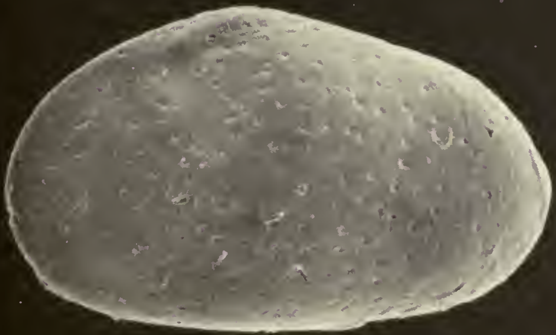
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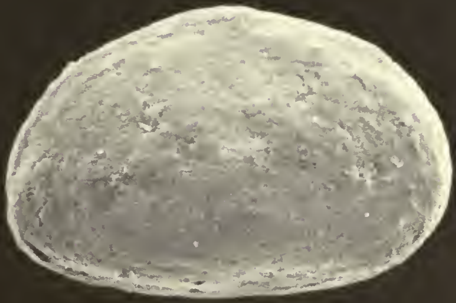
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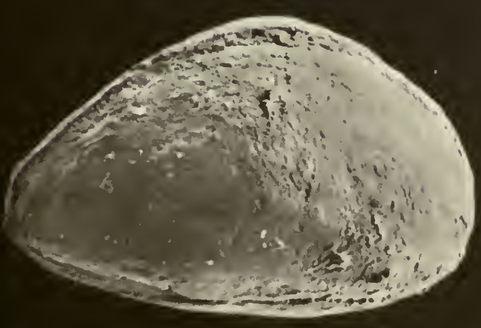
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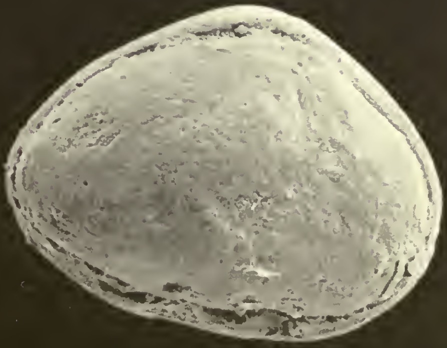
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PLATE 3

FIG. 1. ***Glyptocythere guembeliana*** (Jones). External view, male right valve, lectotype, IN.43493. Originally described as *Cythere guembeliana* by Jones. × 77.

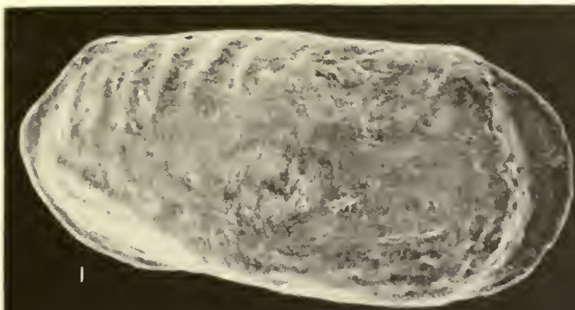
FIG. 2. ***Glyptocythere guembeliana*** (Jones). External view, juvenile right valve, I.1840. Originally described as *Cytheridea trapezoidalis* Terquem by Jones & Sherborn. × 113.

FIG. 3. ***Lophocythere bradiana*** (Jones). Left valve of complete male carapace, lectotype, IN.42372. Originally described as *Cythere bradiana* by Jones. × 101.

FIG. 5. ***Lophocythere bradiana*** (Jones). Right valve of complete male carapace, paralectotype, Io.3627. × 95.

FIG. 6. ***Lophocythere bradiana*** (Jones). Left valve of complete female carapace, paralectotype, Io.3628. × 97.

FIGS. 4, 7, 8. ***Fastigatocythere juglandica*** (Jones). Fig. 4, external view right valve, lectotype, IN.41947, × 75. Figs. 7, 8. Normal pore canals of lectotype, fig. 7 × 2,000, fig. 8 × 5,000. Originally described as *Cythere juglandica* Jones.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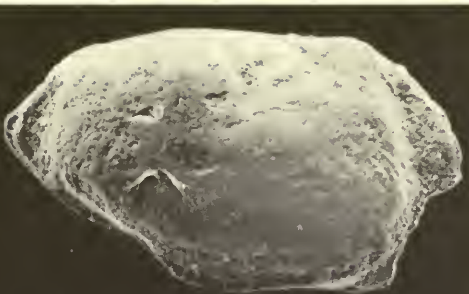
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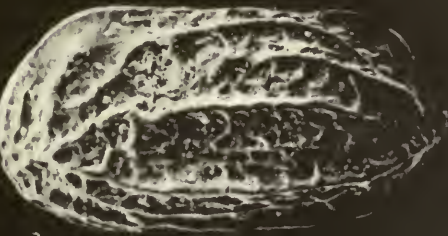
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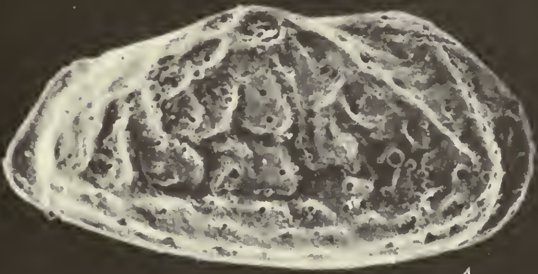
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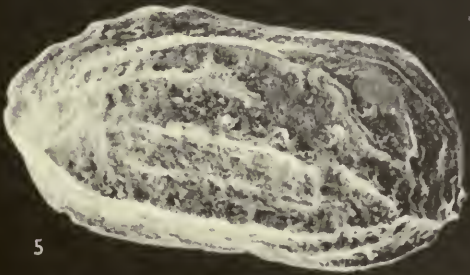
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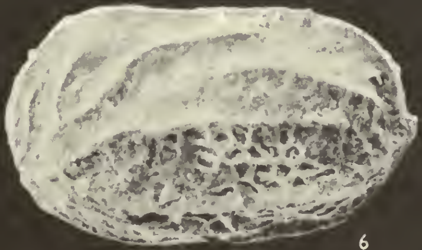
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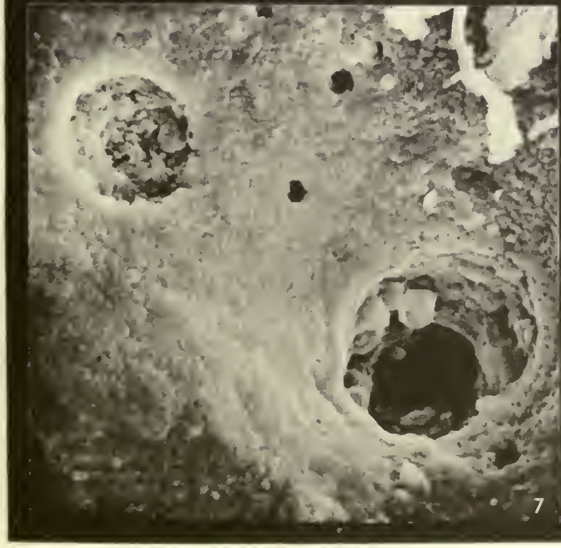
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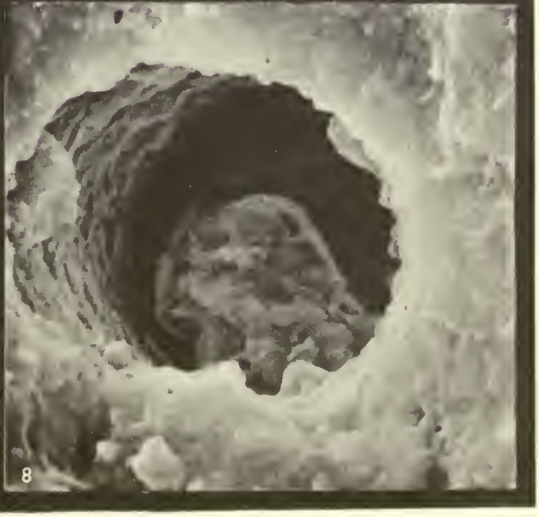
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PLATE 4

FIG. 1. ***Glyptocythere guembeliana*** (Jones). Female right valve and lectotype of *Cytheridea pulvinar* Jones & Sherborn. I.1858. × 85.

FIG. 2. ***Lophocythere bradiana*** (Jones). Right valve of complete male carapace, I.1854. Lectotype of *Cytheridea craticula* Jones & Sherborn. × 100.

FIG. 3. ***Lophocythere bradiana*** (Jones). Male left valve, paralectotype of *C. craticula* Jones & Sherborn. I.1867. × 100.

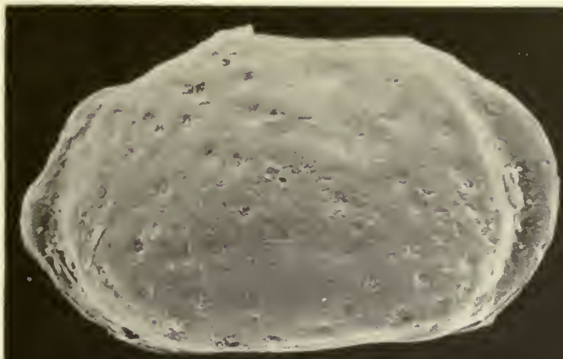
FIG. 4. ***Lophocythere bradiana*** (Jones). Ventral view, female carapace, paralectotype, Io.3629 × 100.

FIG. 5. ***Bairdia hilda*** Jones. Internal view, right valve of paralectotype of *Bairdia fullonica* Jones & Sherborn. Io.3554. × 78.

FIG. 6. ***Bairdia hilda*** Jones. External view, right valve. Lectotype of *B. fullonica* Jones & Sherborn. I.1873. × 78.

FIG. 7. ***Micropneumatocythere subconcentrica*** (Jones). Left valve of lectotype IN.43505. Originally described as *Cythere subconcentrica* Jones. × 100.

FIG. 8. ***Terquemula blakeana*** (Jones). Right valve originally described as *Cytheridea ransversiplicata* Jones & Sherborn. I.1828. × 100.



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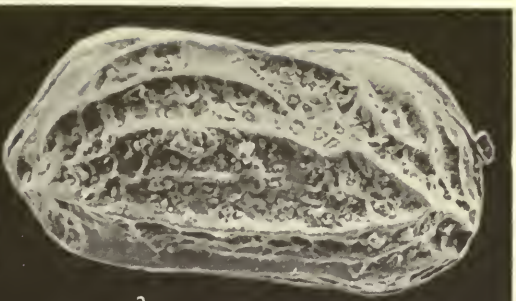

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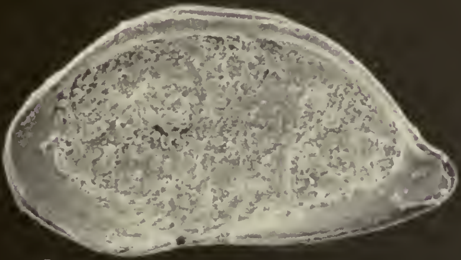

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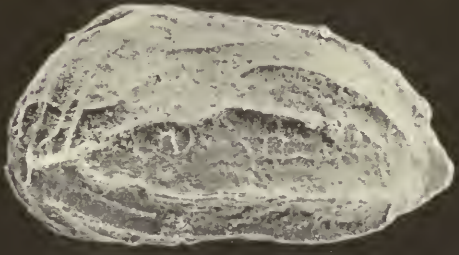

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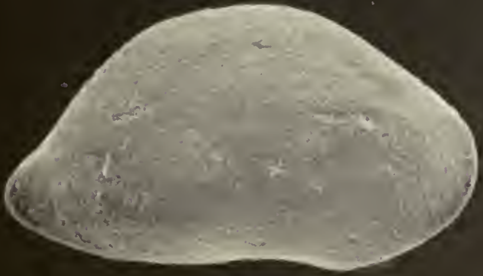

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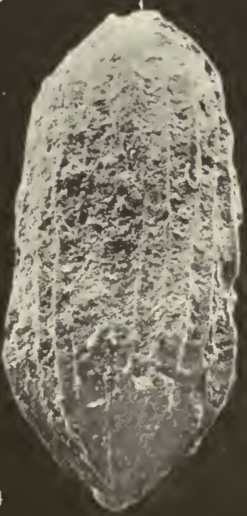

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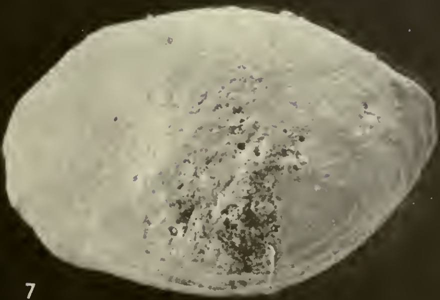

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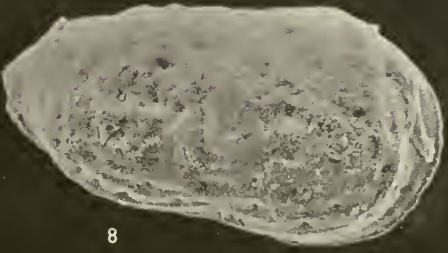

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PLATE 5

Fig. 1. ***Terquemula blakeana*** (Jones). Female left valve, lectotype, IN.41950. Originally described as *Cythere blakeana* Jones. × 100.

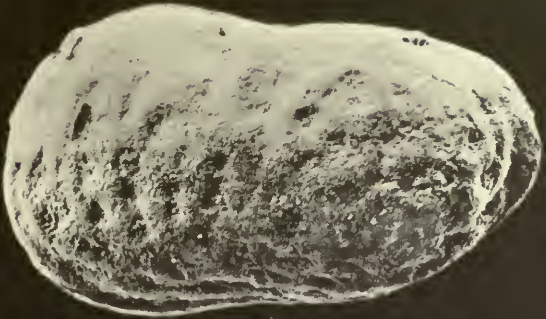
Fig. 2. ***Glyptocythere oscillum*** (Jones & Sherborn). Male left valve, lectotype of *Cytheridea striblita* Jones & Sherborn. Io.3943. × 95.

Figs. 3, 7. ***Cythereis* cf. *blanda*** Kaye. External view, left valve, IN.43502 and right valve of complete carapace, IN.43491. Both specimens originally described as *Cythere* (*Cythereis*) *quadrilatera* (Roemer). × 100.

Figs. 4–6. ***Metacytheropteron drupaceum*** (Jones). Left valve from the Blake Collection, Io.3977. × 100, and left and right views of complete carapace, holotype, IN.43498. × 85. Originally described as *Cythere drupacea* Jones.

Fig. 8. ***Cythere ? tenella*** Jones. Right valve of complete carapace, holotype, IN.43492. × 100.

Fig. 9. ***Cytherella fullonica*** Jones & Sherborn. Left valve of paralectotype, Io.4004. × 105.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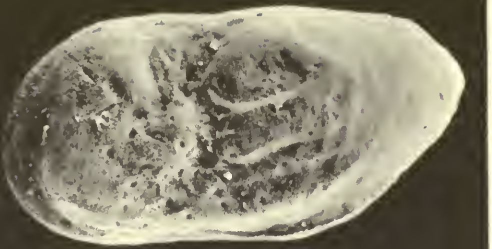
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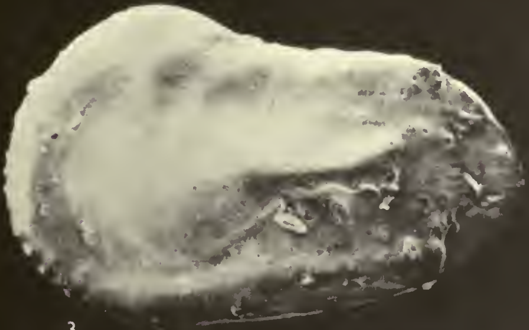
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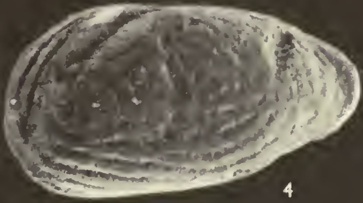
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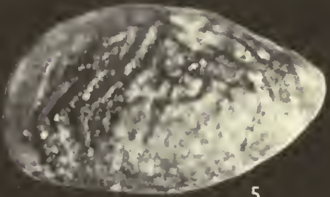
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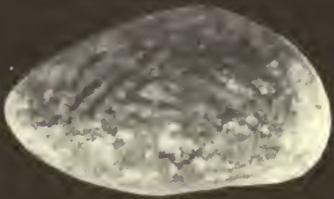
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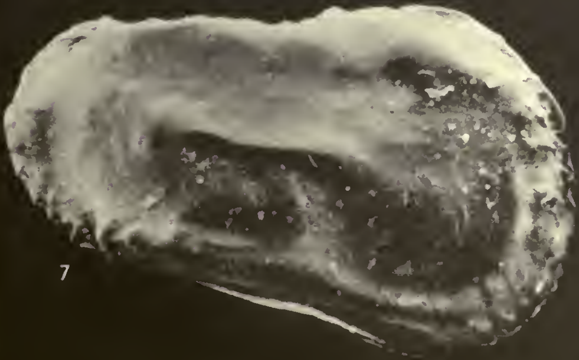
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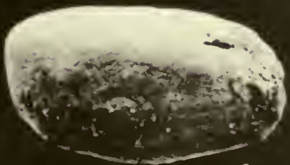
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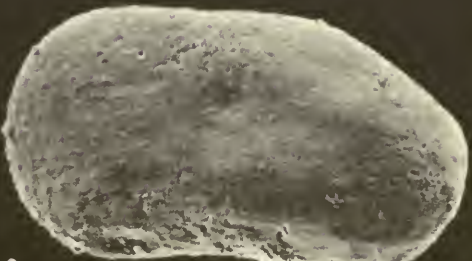
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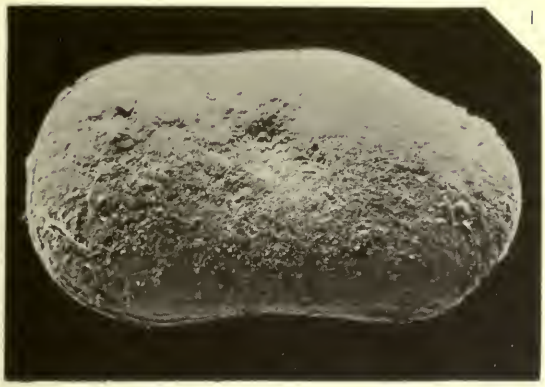
PLATE 6

FIG. 1. ***Cytherella fullonica*** Jones & Sherborn. Left valve, lectotype, I.1857, × 101.

FIGS. 2, 3. ***Cytherelloidea catenulata*** (Jones & Sherborn). Right valve, paralectotype, I.1846, × 100, and left valve, lectotype, I.1876, × 100. Species originally described as *Cytherella catenulata* Jones & Sherborn.

FIGS. 4–7. ***Cytherelloidea refecta*** (Jones & Sherborn). Fig. 4, female left valve, Io.3931 paralectotype, × 100. Figs. 5, 6, male left valve, paralectotype, Io.3932, fig. 5, × 98, fig. 6, anterior ornamentation of same specimen × 5,000. Fig. 7, female right valve, lectotype, I.1850, × 95.

FIG. 8. ***Bairdia sherborni*** sp. nov. Left valve, complete carapace, holotype Io.3913. × 107.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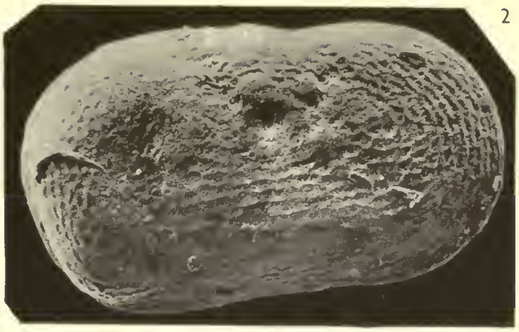
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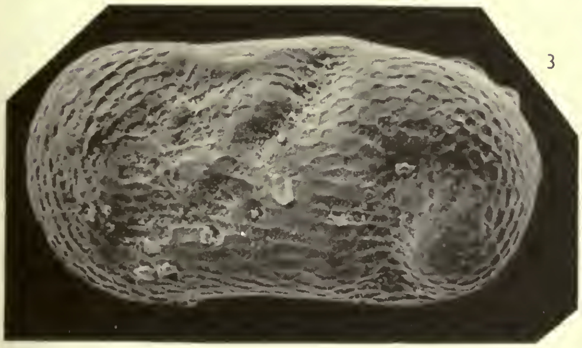
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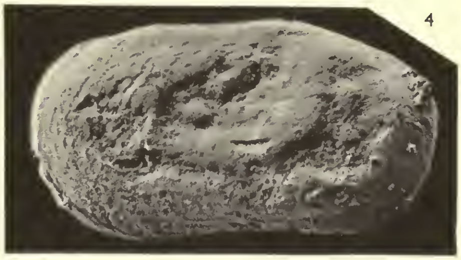
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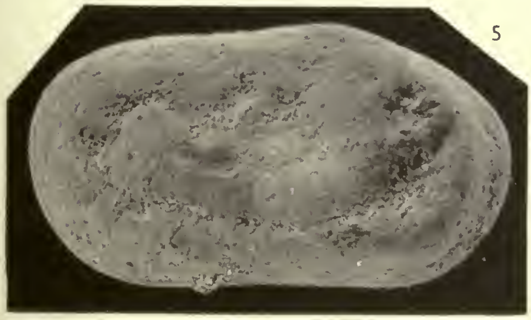
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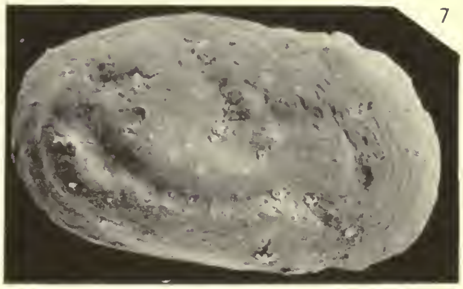
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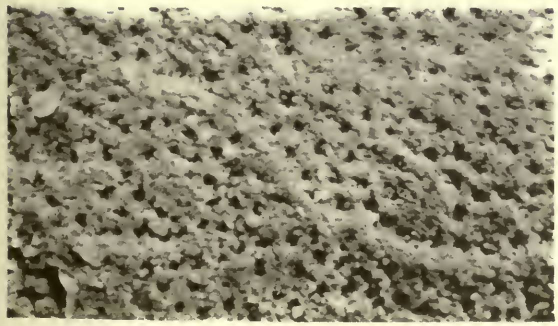
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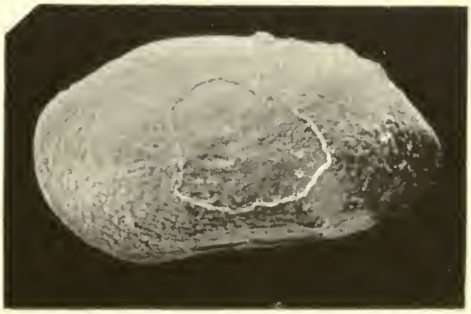
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PLATE 7

FIG. 1. ***Bairdia sherborni*** sp. nov. Right valve, complete carapace, paratype, Io.3557. × 96.

FIG. 2. ***Paracypris terraefullonicae*** (Jones & Sherborn). Right valve of lectotype of *Macrocypris horatiana* Jones & Sherborn. I.1874. × 100.

FIG. 3. ***Monoceratina visceralis*** (Jones & Sherborn). Left valve, holotype, I.1830, × 100. Originally described as *Cytheridea visceralis* Jones & Sherborn.

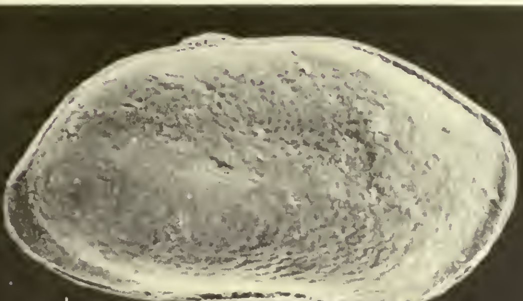
FIG. 4. ***Paracypris terraefullonicae*** (Jones & Sherborn). Left valve, lectotype, I.1875. Originally described as *Macrocypris terrae-fullonicae* Jones & Sherborn. × 100.

FIG. 5. ***Monoceratina vulsa*** (Jones & Sherborn). Damaged left valve, lectotype, I.1842, × 100. Originally described as *Cytheridea vulsa* Jones & Sherborn.

FIG. 6. ***Oligocythereis fullonica*** (Jones & Sherborn). Right valve of complete carapace, lectotype, I.1871. Originally described as *Cythereis fullonica* Jones & Sherborn. × 111.

FIG. 7. ***Schuleridea*** (***Eoschuleridea***) ***horatiana*** (Jones & Sherborn). Male right valve, lectotype, I.1852. Originally described as *Cytheridea horatiana* Jones & Sherborn. × 56.

FIG. 8. ***Asciocythere obovata*** (Jones & Sherborn). Right valve of complete carapace, paralectotype, Io.3938, × 100. Originally described as *Cytheridea obovata* Jones & Sherborn.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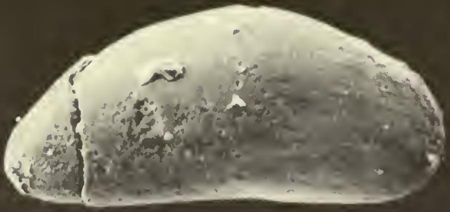
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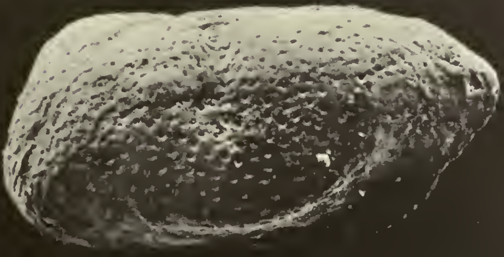
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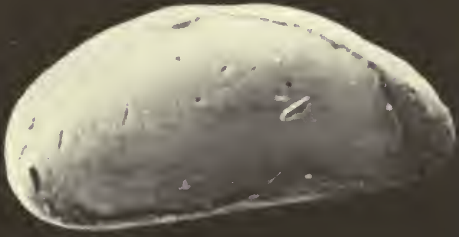
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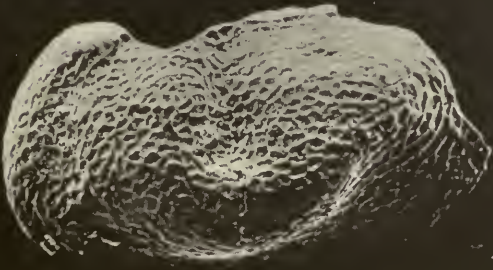
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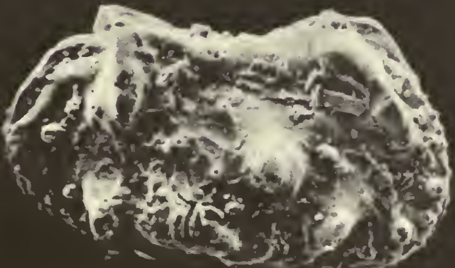
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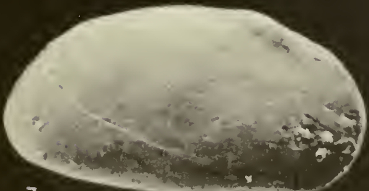
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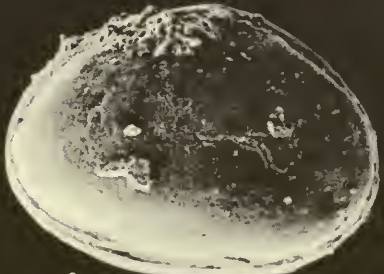
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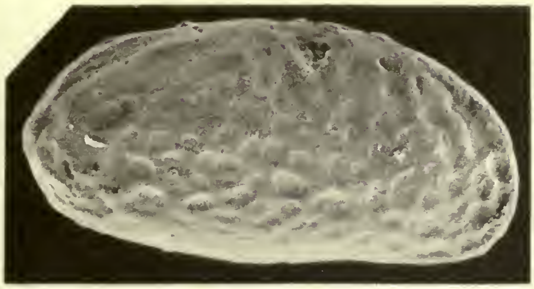
PLATE 8

FIG. 1. ***Eocytheridea*** sp. Right valve, Io.3906, × 85.

FIGS. 2, 7. ***Asciocythere obovata*** (Jones & Sherborn). Left valve of complete carapace, Io.3939, × 100 and part of shell surface showing normal pore canals, × 650.

FIG. 3. ***Asciocythere obovata*** (Jones & Sherborn). Right valve, lectotype, I.1836. × 100.

FIGS. 4–6. ***Praeschuleridea subtrigona*** (Jones & Sherborn). Male right valve, lectotype, I.1838, × 98; right valve, female carapace, paralectotype, Io.3937, × 100 and left valve, male carapace, paralectotype, Io.3936. × 100.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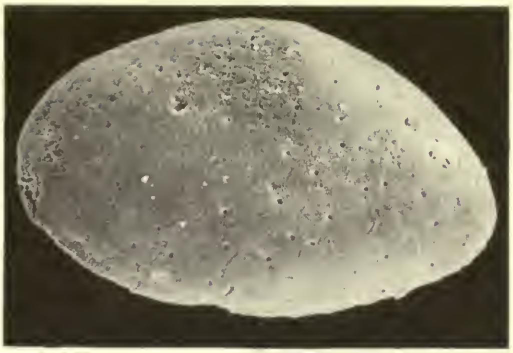
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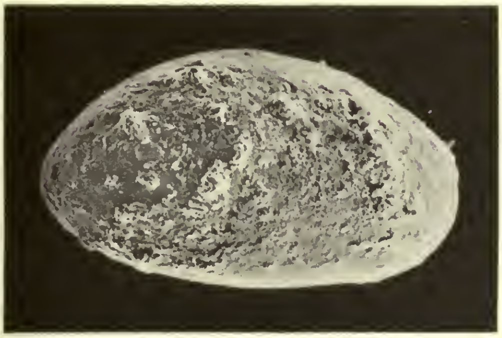
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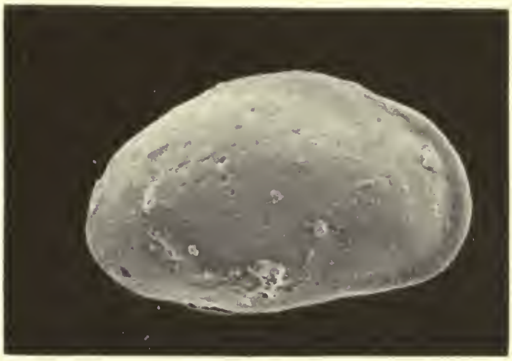
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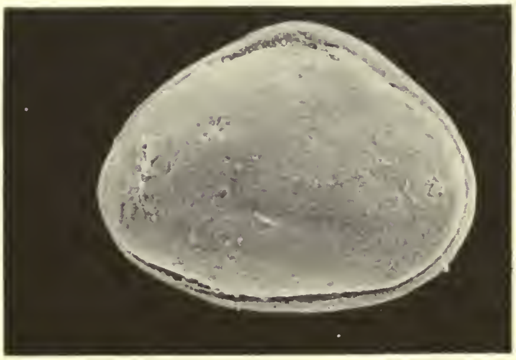
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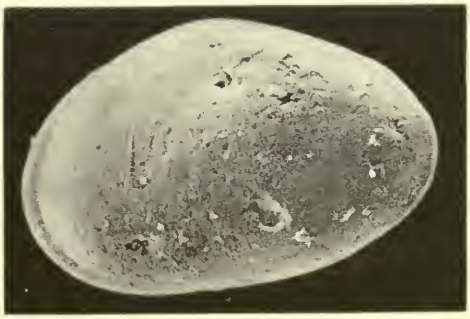
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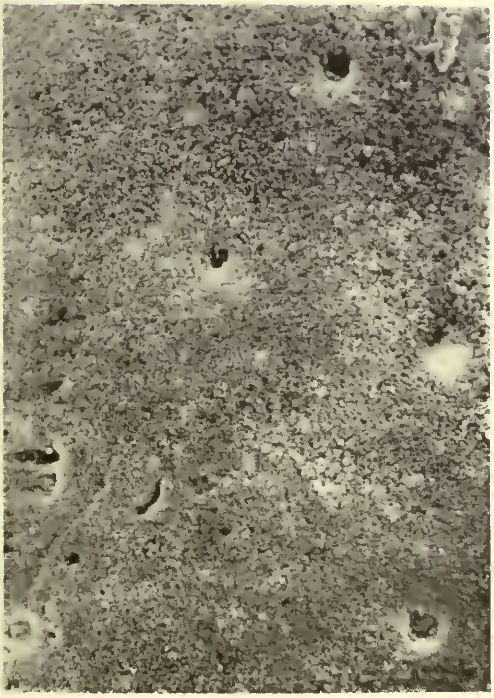
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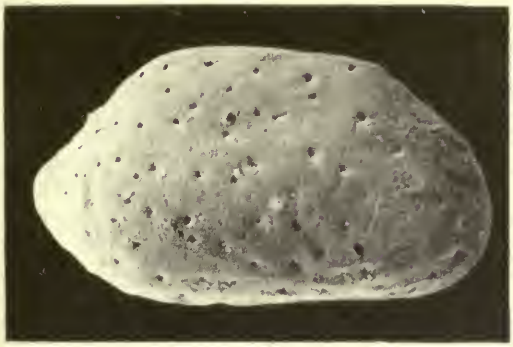
PLATE 9

Figs. 1–8. **Hadrocytheridea dolabra** (Jones & Sherborn). Figs. 1, 4. External and internal views, female right valve, lectotype, I.1851, × 100. (Lectotype of *Cytheridea dolabra* Jones & Sherborn.) Fig. 2. Female left valve *Cytheridea pentagonalis* of Jones & Sherborn), Io.3929, × 100. Fig. 3. Internal view male right valve (*Cytheridea parallela* of Jones & Sherborn), paralectotype, Io.3926, × 100. Fig. 5. Male left valve, paralectotype, I.1844 (lectotype of *Cytheridea puteolata* Jones & Sherborn), × 100. Fig. 6. Female left valve, paralectotype, I.1866 (holotype of *Cytheridea pentagonalis* Jones & Sherborn), × 100. Fig. 7. Male right valve, complete carapace, paralectotype, I.1859 (lectotype of *Cytheridea parallela* Jones & Sherborn), × 100. Fig. 8. Right valve, possibly juvenile instar of *H. dolabra* (lectotype of *Cytheridea ignobilis* Jones & Sherborn), I.1868, × 100.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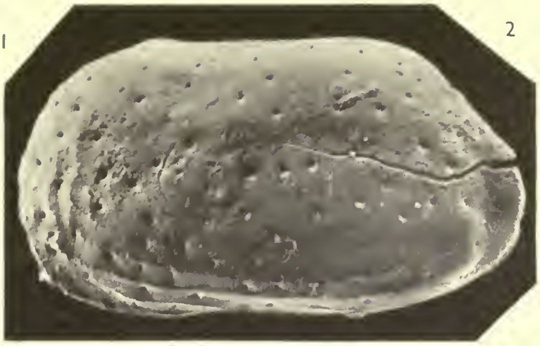
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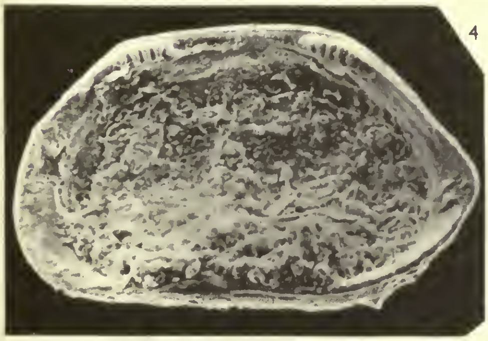
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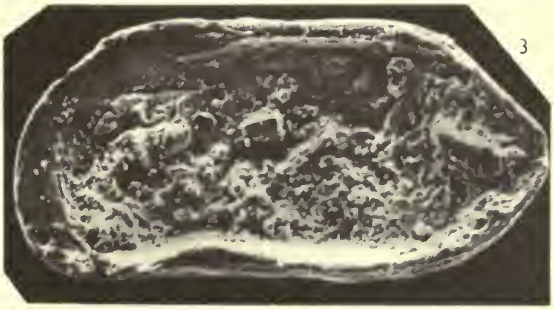
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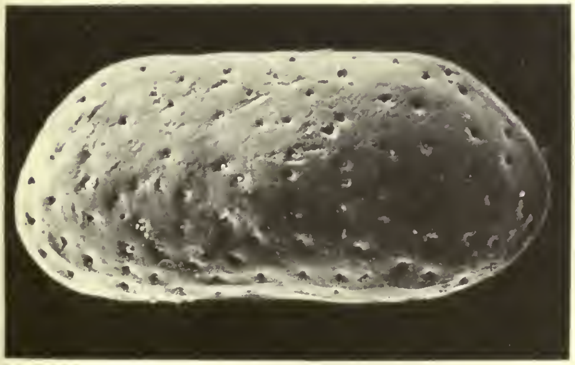
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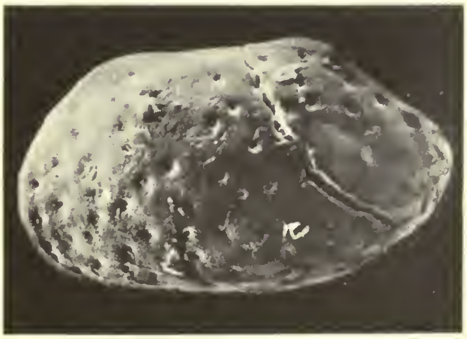
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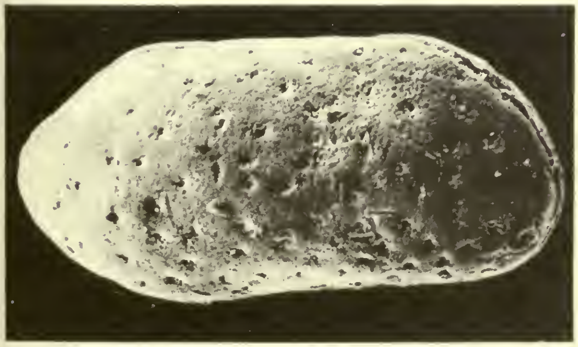
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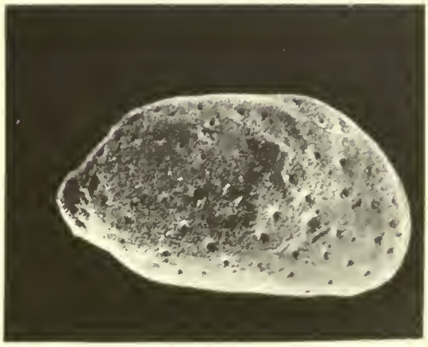
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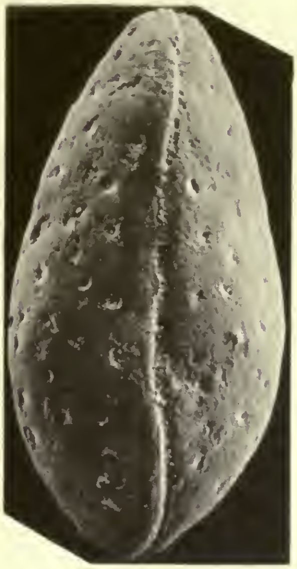
PLATE 10

FIG. 1. ***Hadrocytheridea dolabra*** (Jones & Sherborn), Dorsal view, male carapace, paralectotype, I.1859 (lectotype of *Cytheridea parallela* Jones & Sherborn). × 100.

FIGS. 2, 7, 8. ***Caytonidea terraefullonicae*** (Jones & Sherborn). Dorsal view, female carapace, paralectotype, Io.3920, × 100; female left valve, lectotype, I.1869, × 100 and female right valve, paralectotype, Io.3919, × 100. Species originally described as *Cytheridea terraefullonicae* Jones & Sherborn.

FIGS. 3–6. ***Rectocythere sugillata*** (Jones & Sherborn). Figs. 3, 6, external and internal view, left valve lectotype, I.1855, × 100. Figs. 4, 5, external and internal view, right valve paralectotype, Io.3930, × 100. Species originally described as *Cytheridea sugillata* Jones & Sherborn.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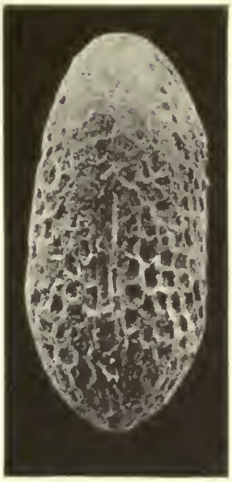
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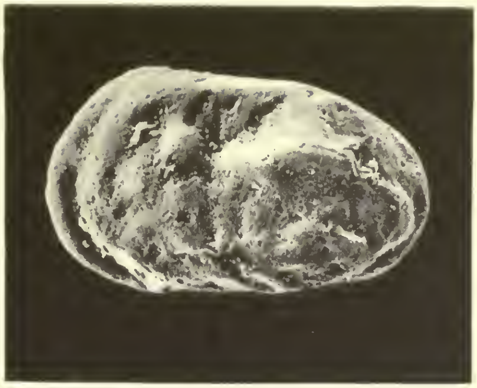

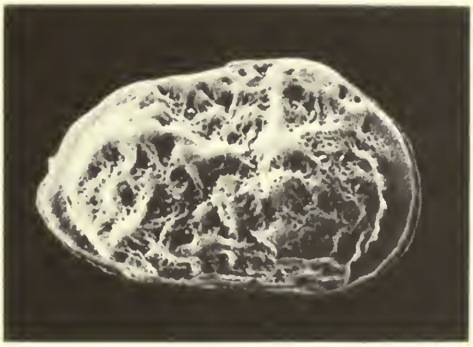
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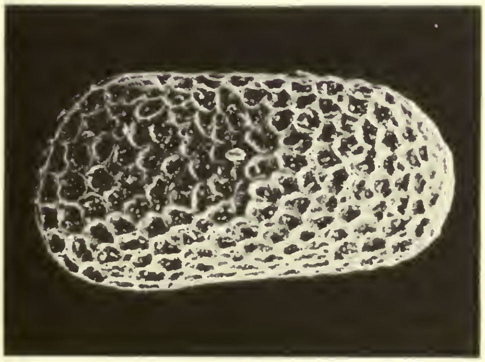
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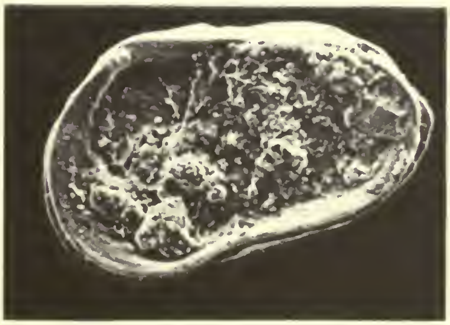
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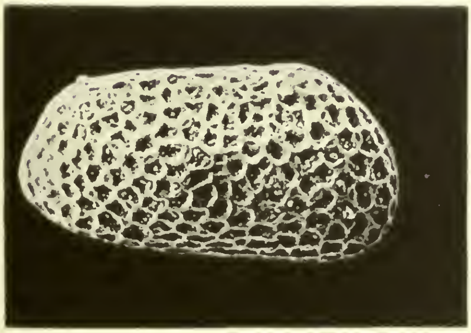
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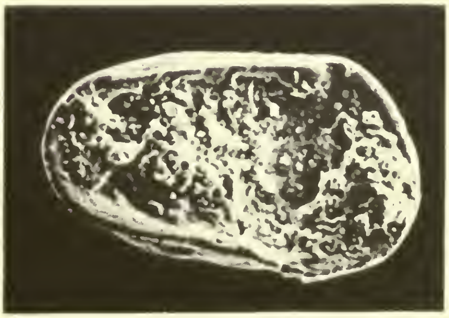
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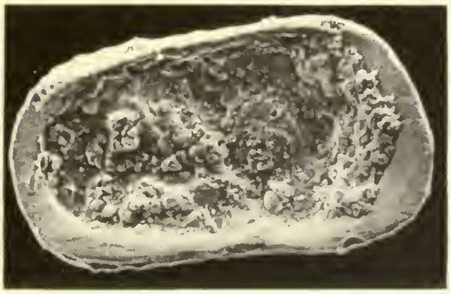
PLATE 11

Figs. 1–3. ***Caytonidea terraefullonicae*** (Jones & Sherborn). Internal view, female left valve, lectotype, I.1869, × 100; internal view × 100 and surface ornamentation × 750 of female right valve, paralectotype, Io.3919.

Figs. 4–6. ***Acanthocythere sphaerulata*** (Jones & Sherborn). Right valve, complete female carapace × 100 and enlargement of surface ornamentation × 2,800 and × 500. Holotype, I.1835. Species originally described as *Cythere sphaerulata* Jones & Sherborn.



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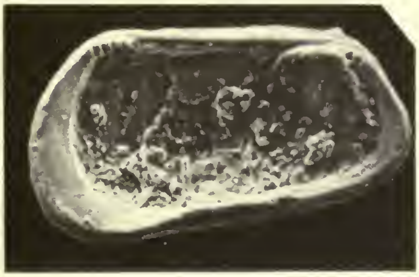

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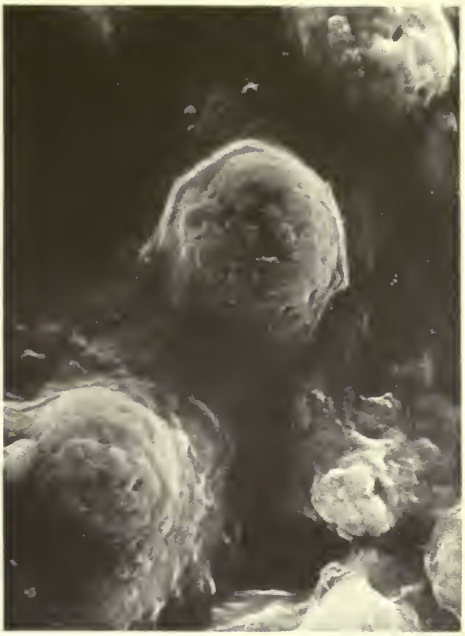

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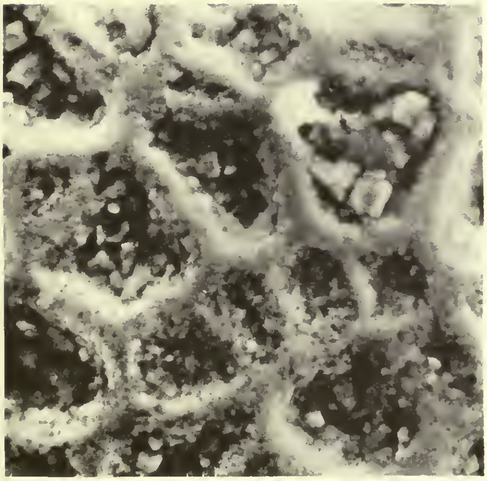

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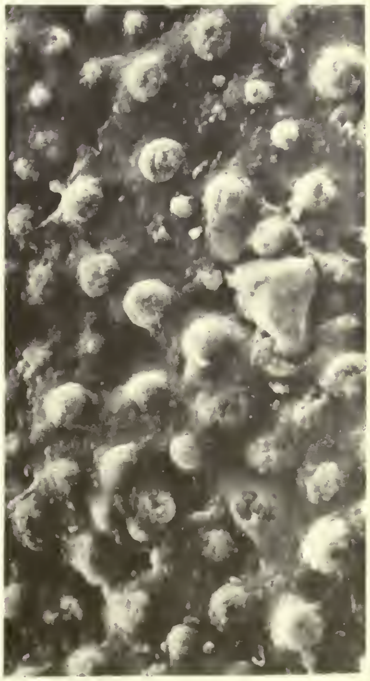

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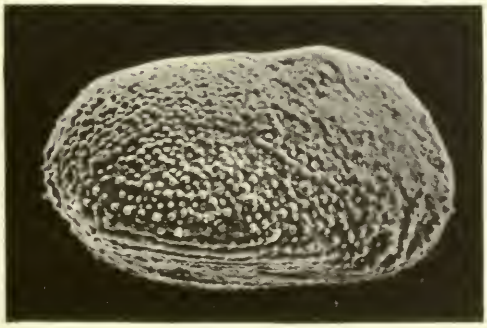

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PLATE 12

FIG. 1. ***Glyptocythere persica*** (Jones & Sherborn). Right valve, holotype, I.1834, × 100. Originally described as *Cytheridea persica* Jones & Sherborn.

FIG. 2. ***Glyptocythere oscillum*** (Jones & Sherborn). Female right valve, lectotype, I.1849 (holotype of *Cythere oscillum* Jones & Sherborn), × 105.

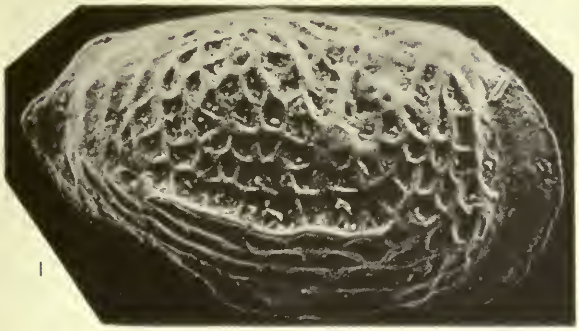
FIG. 3. ***Fastigatocythere juglandica*** (Jones & Sherborn). Female left valve, I.1872, × 92. Originally described as *Cythere juglandica* var *major* by Jones & Sherborn.

FIGS. 4, 6. ***Lophocythere acutiplicata*** (Jones & Sherborn). Left valve, female carapace, lectotype, I.1863, × 112 and internal view, female right valve, paralectotype, I.1847, × 103.

FIG. 5. ***Lophocythere ostreata*** (Jones & Sherborn). Right valve, holotype, I.1833, × 85. Originally described as *Cytheridea ostreata* Jones & Sherborn.

FIG. 7. ***Lophocythere fulgurata*** (Jones & Sherborn). Right valve, lectotype, I.1832, × 85. Originally described as *Cytheridea fulgurata* Jones & Sherborn.

FIG. 8. ***Lophocythere septicostata*** Bate. Female right valve, I.1843, × 100. Originally described as *Cytheridea bradiana* Jones & Sherborn.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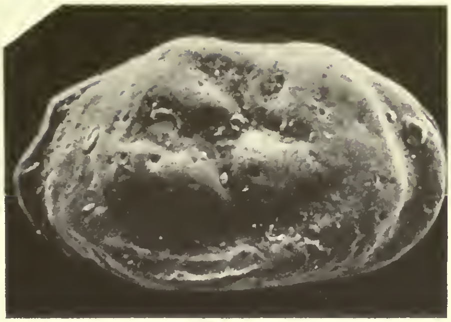
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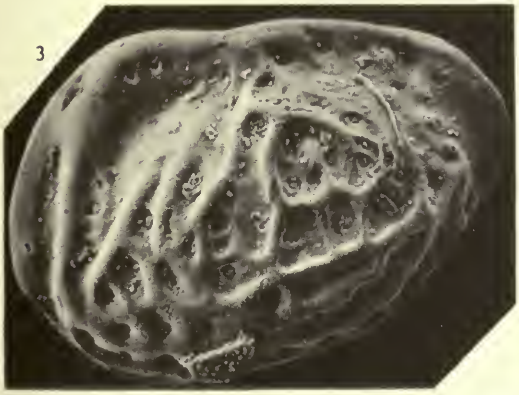
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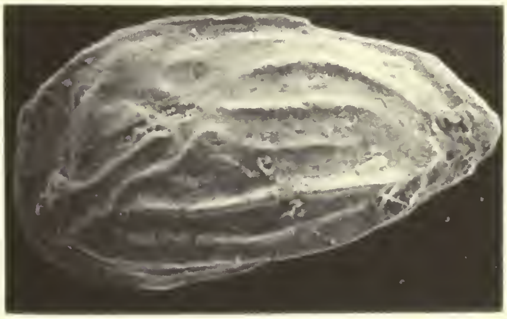
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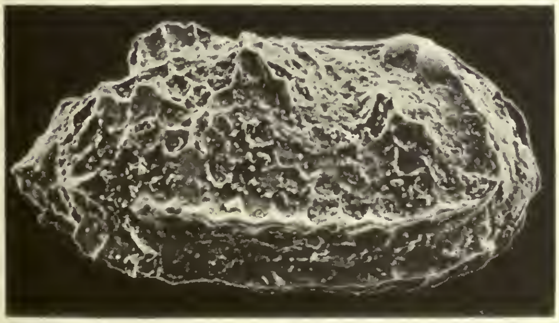
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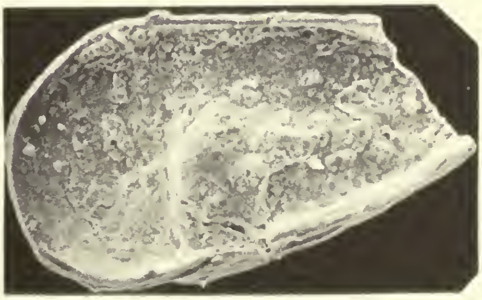
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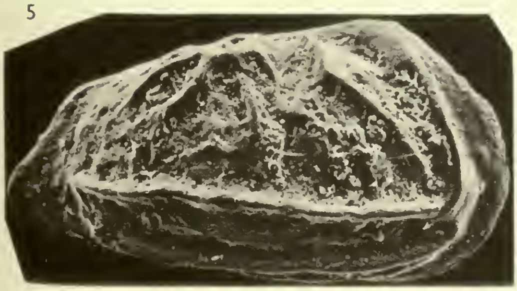
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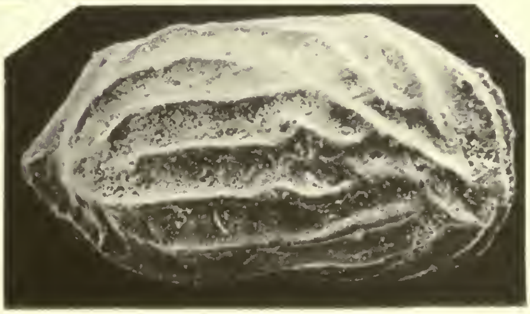
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PLATE 13

FIG. 1. ***Micropneumatocythere limaciformis*** (Jones & Sherborn). Right valve, holotype, I.1831. Originally described as *Cytheridea limaciformis* Jones & Sherborn. × 85.

FIG. 2. ***Progonocythere stilla*** Sylvester-Bradley. External view, left valve, Io.3657. × 114.

FIG. 3. ***Cytheridea aequabilis*** Jones & Sherborn. Left valve of complete carapace, holotype, I.1864. × 80.

FIG. 4. ***Cythere corrosa*** Jones & Sherborn. Right valve of complete carapace, holotype, I.1865. × 100.

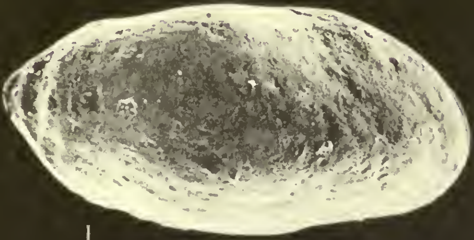
FIG. 5. ***Cytheridea coarctata*** Jones & Sherborn. Left valve, holotype, I.1841. × 100.

FIG. 6. ***Cytheridea eminula*** Jones & Sherborn. Left valve, lectotype, I.1839. × 100.

FIG. 7. ***Cytheridea spinifastigiata*** Jones & Sherborn. Left valve, holotype, I.1861. × 100.

FIG. 8. ***Cytheridea punctiputeolata*** Jones & Sherborn. Right valve, holotype, I.1856. × 85.

FIG. 9. ***Cytheridea spinigyrata*** Jones & Sherborn. Right valve, holotype, I.1860. × 100.



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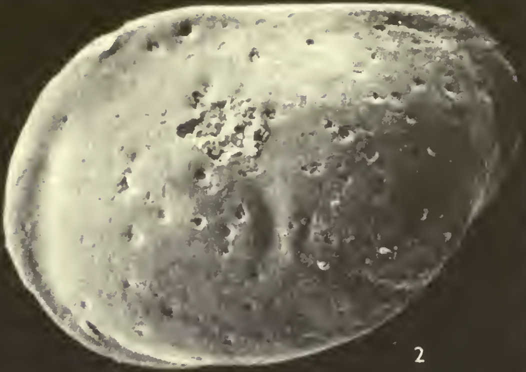

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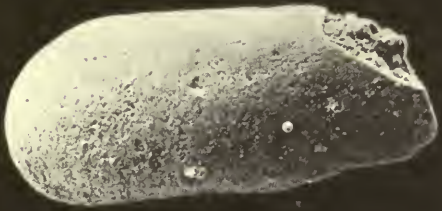

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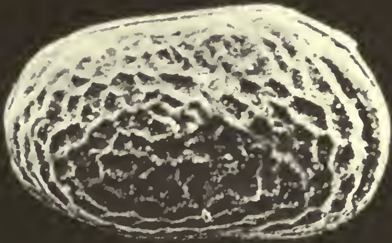

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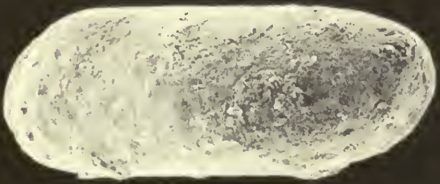

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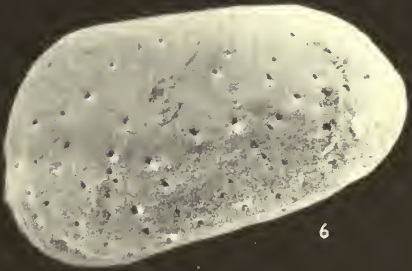

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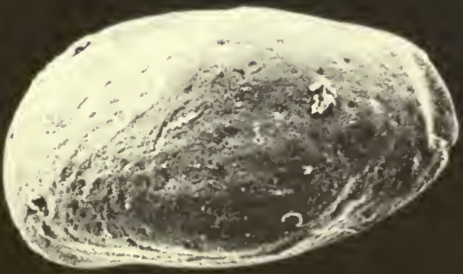

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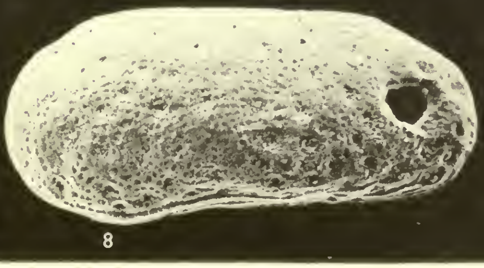

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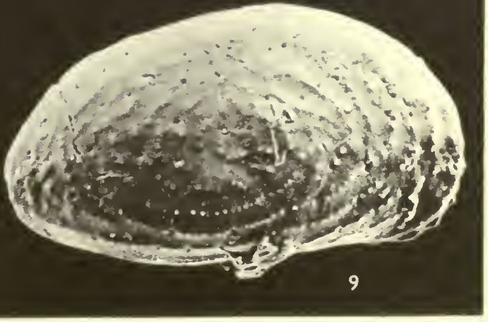

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PLATE 14

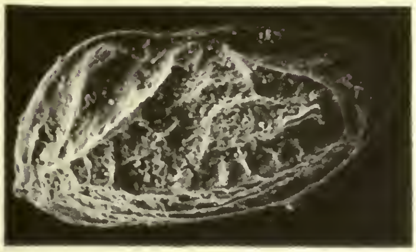
FIGS. 1, 3. ***Ektyphocythere parva*** Oertli. Left valve, male carapace, Io.3983, × 115 and right valve, female carapace, Io.3982, × 114.

FIGS. 2, 4, 9. ***Hekistocythere venosa*** sp. nov. Left valve, paratype, Io.3996, × 195; right valve of complete carapace, holotype, Io.3995, × 190, and internal view, left valve, paratype, Io.4012, × 150.

FIG. 5. ***Platycythere*** sp. Right valve of complete carapace, Io.3992, × 110.

FIG. 6. ***Looneyella monticula*** (Jones). Left valve of complete carapace, holotype, I.5872, from the Cretaceous Bear River Formation, Wyoming. × 97.

FIGS. 7, 8. ***Looneyella subtilis*** Oertli. Left valve of complete male carapace, Io.3957, × 144, and right valve of complete male carapace, Io.3956, × 144.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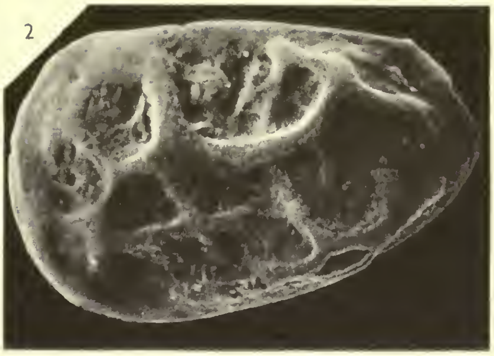
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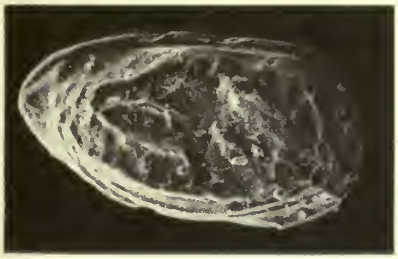
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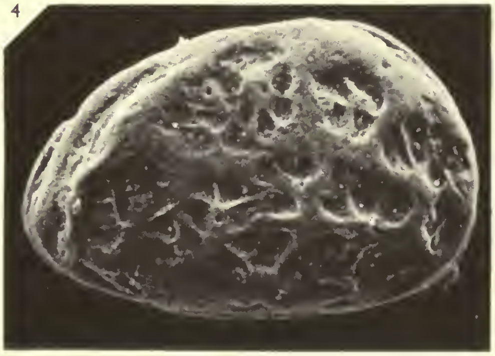
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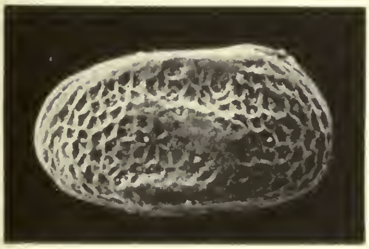
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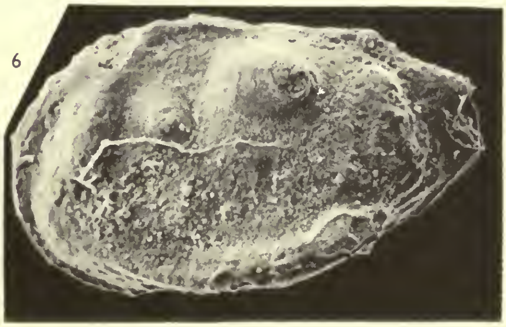
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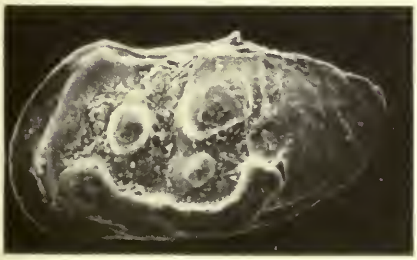
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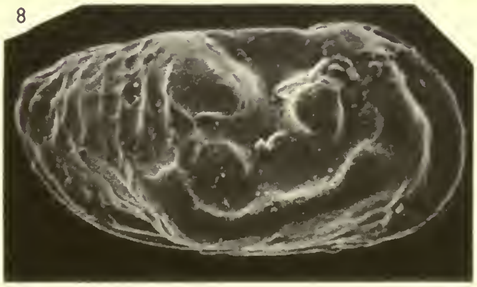
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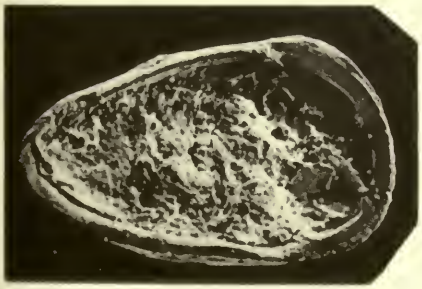
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PLATE 15

Fig. 1. ***Orthonotacythere*** sp. nov. Right valve of complete carapace, Io.3993, × 144.

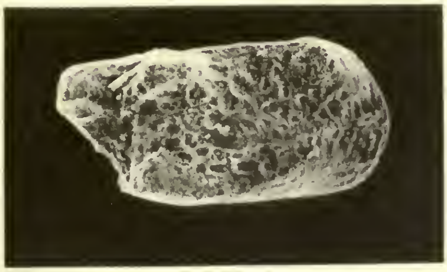
Figs. 2, 8. ***Parariscus bathonicus*** Oertli. Left valve of complete carapace, Io.3959, × 144 and dorsal view of complete carapace, Io.3860, × 144.

Fig. 3. ***Cytheridea retorrida*** Jones & Sherborn. Left valve of complete carapace, Io.3923. × 108.

Figs. 4, 5, 9, 10. ***Paracytheridea ? blakei*** sp. nov. Fig. 4, muscle scars of paratype, Io.4015, as viewed externally, × 250; fig. 5, dorsal view, complete carapace, paratype, Io.4016, × 200; fig. 9, right valve, complete carapace, holotype, Io.4001, × 200 and fig. 10, left valve, complete carapace, paratype, Io.4014, × 200.

Fig. 6. ***Cytherura mediojurassica*** sp. nov. Dorsal view of complete carapace, × 200.

Fig. 7. ***Hekistocythere venosa*** sp. nov. Dorsal view of complete carapace, holotype, Io.3995. × 190.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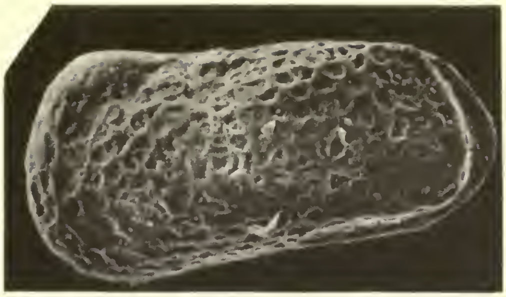
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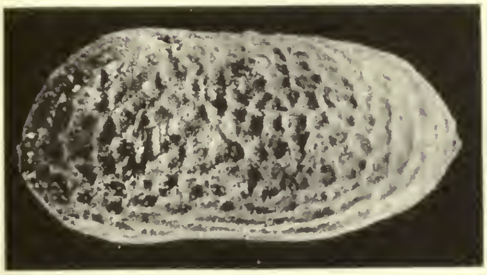
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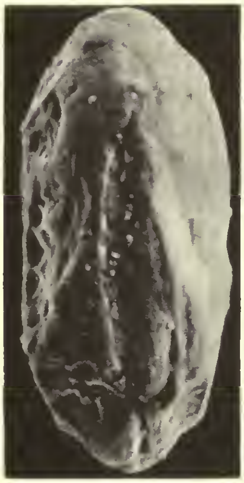
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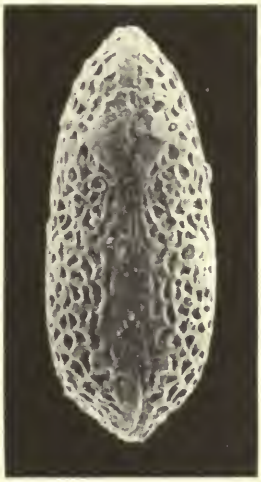
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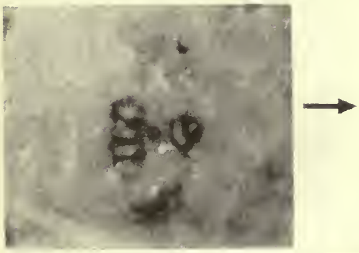
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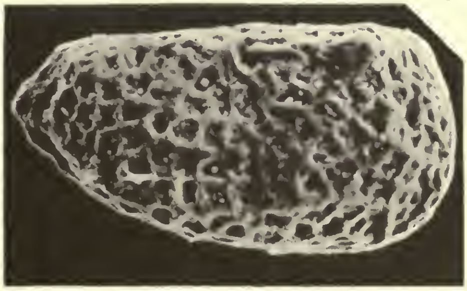
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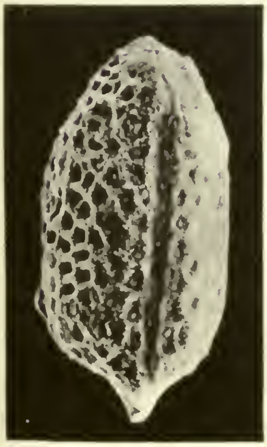
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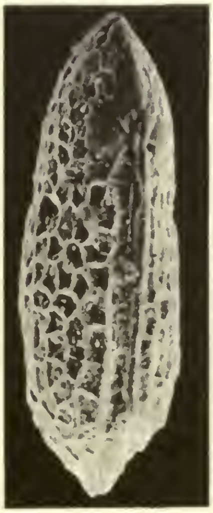
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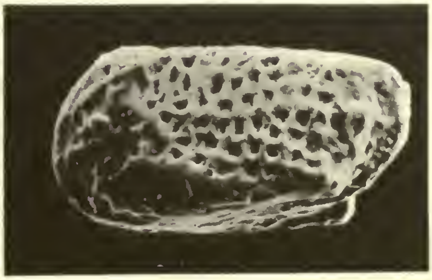

10

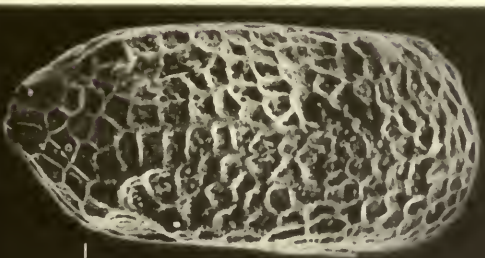
PLATE 16

Figs. 1, 2. ***Cytherura mediojurassica*** sp. nov. Right valve of complete carapace, holotype, Io.4121, × 190 and left valve of complete carapace, paratype, Io.4122, × 195.

Fig. 3. ***Trachycythere*** sp. Left valve, Io.3966, × 114.

Figs. 4, 9. ***Polycope fungosa*** sp. nov. Left valve, juvenile carapace, paratype, Io.3953, × 112, and left valve of complete adult carapace, holotype, Io.3951, × 112.

Figs. 5–8. ***Cytherura bathonica*** sp. nov. Fig. 5, left valve of complete carapace, paratype, Io.4018, × 195; fig. 8, ornamentation of same specimen, × 1,200; fig. 6, dorsal view of complete carapace, paratype, Io.4019, × 194; fig. 7, right valve of complete carapace, holotype, Io.4017, × 195.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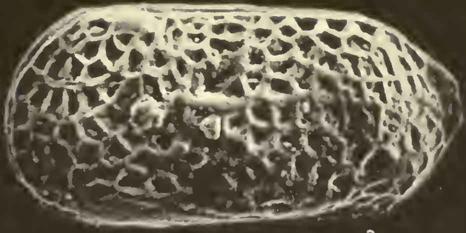
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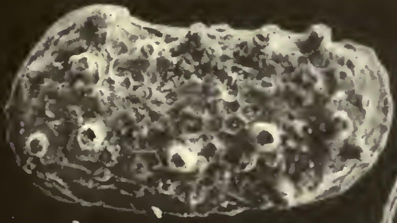
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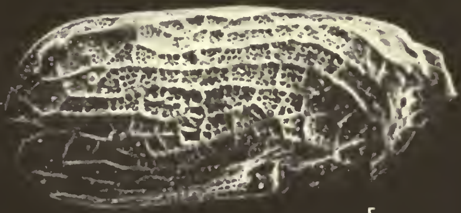
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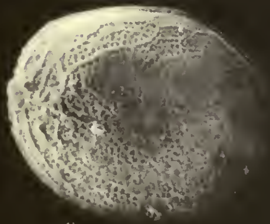
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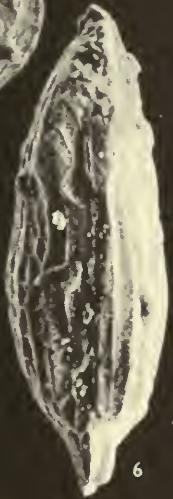
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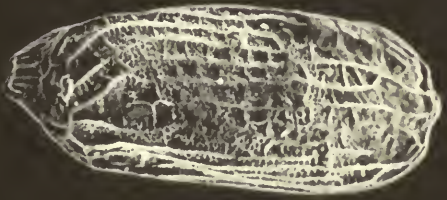
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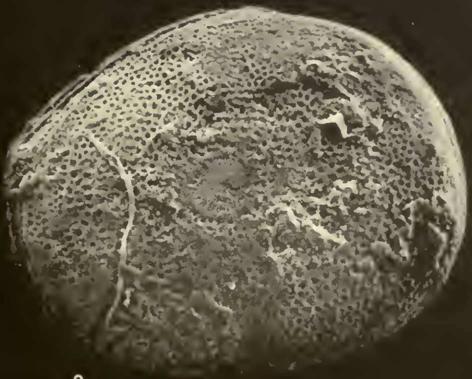
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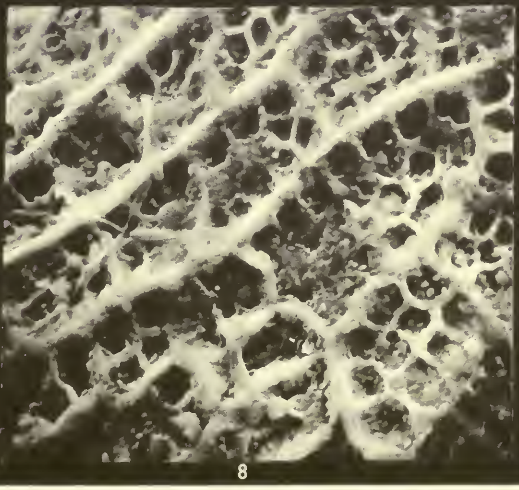
8

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30 MAY 1969

INDEX TO VOLUME XVII

New taxonomic names and the page numbers of the principal references are printed in **Bold** type. An asterisk (*) indicates a figure.

Acanthinocyathidae **306**, 372
Acanthinocyathus 306, **308**
  apertus 306, **307*–308**; Pl. 2, figs. 1–4
  transiens 306
Acanthistius 87
Acanthocyathus 306
  apertus 306, 307
Acanthocythere 411
  sphaerulata **411**; Pl. 11, figs. 4–6
Acanthuroidei 87, 92
Achomosphaera 174
  ramulifera **174–175**; Pl. 10, fig. 7
  reticulata 175
  sagena **175**
Acritarcha 107
Acrogaster **73**, 75
  brevicostatus 73
  daviesi 73
  heckeli 73*
  parvus 73
Acrognathus 82, 83, 98
Acroporidae 13
Acrostichopteris ruffordi 238
Adnatosphaeridiaceae 171
Adnatosphaeridium 171, 172
  chonetum **171–172**; Pl. 10, figs. 11, 12
Agastrocyathus 342
Aipichthyidae 62, 92, 97, 100
Aipichthys 49, **62–63**, 65, 66, 84, 85, 87, 88, 93, 94, 95, 97, 98, 99
  minor 63, 64*, 65*
  nuchalis 63
  pretiosus 62
  velifer 63, 66, 99
Ajacicyathacea 372
Ajacicyathida 305
Ajacicyathidae 308
Ajacicyathus 310, 345, 369
  walliseri 312, 314
  (*Ajacicyathellus*) 310
Alataucyathinae **338**, 340
Alataucyathus **340**, 369, 372
Alataucyathidae **338**
  (*Urcyathus*) 334
  jaroschevitshi 340
  (*Alataucyathus*) 338, **340**
  (Anaptyctocyathus) 299, 372
  cribripora **340–341**, 342, 372; Pl. 11, figs. 1, 3
  excellenthis 340
  flabellus 299, 340, **341–342**, 372; Pl. 10, fig. 1
  minimiporus 340
  verschkhovskajae 340
Albula 54
Alectis 98
Alepocephalus 84
Alethopteris goepperti 228
Algites 221
  catenelloides 223
  valdensis 221
Allothrissops 84, 85, 91
Alphacyathus **305**, 310, 369
  annularis 305
  cf. *annularis* **305–306**; Pl. 1, fig. 2
Alveolites heteropora 12
Amphiblestrella 20
  elegans **20–21**, 41; Pl. 4, figs. 1–3
Amphiblestrum 21
  elegans 20
Anabantidae 95
Anabantoidei 89, 93
Anasca 13
Anemia 232
  adiantifolia 232
  cuneata 232
Anomalopidae 68, 95, 96
Anomozamites schaumburgense 242
Anoplogaster 68
Anoplogasteridae 68, 99
Antigonia 94, 96
Aptea polymorpha 171
  cf. *polymorpha* 170, 171
Apteodinium **130**
  granulatum 121, **130–131**; Pl. 3, figs. 5, 6
Archaeocyatha 342, 359
Archaeocyathellus 308, 310
  (*Stapicyathus*) **308**
  stapipora 308, **309**, 369; Pl. 1, fig. 5
  yukonensis 308
Archaeocyathidae 346
Archaeocyathus 344, 346, 372

  acutus 312
  atlanticus 345*, 346
  dissepimentalis 358, 359
  floreus 310
  ichnusae 318
  infundibulum 318
  irregularis 348
  magnipora 311
  retesepta 364, 366
  retevallum 314, 315
  retezona 316
  robustus 311
  stapipora 308, 309
  subacutus 312
  trachealis 318
  tracheodentatus 318, 319
  tubavallum 318
  (*Protocyathus*) *stapipora* 309
Archaeolynthus 302
  porosus 303
Archaeopharetra 312, 342
Ardrossacyathus 354
Areoligeraceae 166
Argentina 54, 86
Arripidae 87
Arripis 87
Asciocythere 404
  acuminata 404
  lacunosa 404
  obovata **404–405***; Pl. 7, fig. 8; Pl 8, figs. 2, 3, 7
Ascodinium hialinium 110
Ascophora 13
Aspidistes **235**
  sewardi 235, **236–237***; Pl. 6, figs. 3, 4
  thomasi 235, 236
Aspidium 235
Asterocyathus 325
Asterotumulus 338
Aulacephalodon 286
Aulolepididae 51, 83
Aulolepis **53–54**, 55, 63, 83, 84, 86, 87, 93, 98, 99
  typus 52*, 53*
Aulopodidae 81
Aulopus 54, 68, 81, 83, 84, 86, 88, 93, 98

Bactrellaria 24
  rugica **24–25**, 41; Pl. 2, figs. 9–14
Bairdia 383, 397
  fullonica 383, 397; Pl. 4, figs. 5, 6
  harrisiana 385
  hilda 383, 384, 385, **397–398**; Pl. 1, figs. 5, 6; Pl. 4, figs. 5, 6
  juddiana **383–384**, 395; Pl. 1, fig. 7
  jurassica **384–385**; Pl. 2, figs. 1, 2
    tenuis 384, 385; Pl. 2, fig. 2
  sherborni 398; Pl. 6, fig. 8; Pl. 7, fig. 1
  trigonalis 386, 395; Pl. 2, fig. 7
Bairdiacea 383, 397
Biardiidae 383, 397
Baltisphaeridium armatum 153
  bifidum 165
  ferox 159
  longifurcatum 158
  multifurcatum 152
  pseudohystrichodinium 163
Barroisina trifossata 37, 38
Barysoma 290
Bathymaster 91
Bathysoma 49, **78–81**, 96, 97, 100
  lutkeni 78, 79*, 81, 97
Beaufort series 291
Becklesia 244
  anomala **244–245***, 248
  sulcata 247*–248, 249; Pl. 2, fig. 6
Bedfordcyathus 299, 355, 359
  irregularis 359
Beisselina 39, 40
  flabellata 40
  striata **39–40**, 41; Pl. 8, figs. 3, 4
Beisselinopsis 40
  flabellata **40**, 41; Pl. 8, figs. 1, 2
  marginata 40
Belontiidae 95
Bennettitales 211
Berenicea 15
  sp. **15**, 41
Berycidae 68, 88, 94, 95, 96, 99
Beryciformes 49, 56, 81, 83, 86, 87, 88, 92, 95, 96, 97, 98, 99
Berycoidei 49, 63, **67–69**, 82, 84, 86, 87, 92, 93, 94, 95, 96, 97, 99, 100
Berycopsis **57–58**, 59, 92
  elegans 57*, 58
  geramanus 58
Beryx 94
Biflustra 20, 22
  meudonensis 26
  radula 21
  simplex 20
  tesselata 25, 26
  unipora 19
Brama 87
Bramidae 87
Branchiostegidae 87
Branchiostegus 87
Bronchocyathidae **317–318**, 319, 372
Bronchocyathus 317, 318, 319, 372
  dentatus 321
  trachealis 318
  tracheodentatus 319
Brycon 84
Bryophyta 210, 211, 218
? Bryophyte leaf **218**, 221, 222*
Bythocypris winwoodiana 395
Bythocytheridae 399

Callaiosphaeridium **151**
  asymmetricum **152**; Pl. 6, fig. 6

Cambrocyathellus 354
Cambrocyathus 354, 356, 370
  profundus 357*, 358
Camptocythere lincolnensis 410
Canningia 140
  rotundata 141
Cannosphaeropsis 172
  choneta 171
Caproberyx **76–77**, 78, 94, 95
  pharsus 77
  polydesmus 77
  superbus 76*
Caproidae 93, 96
Capros 96
Carangidae 92
Carpodinium 129
  obliquicostatum **129**; Pl. 1, figs. 3, 4
Cassandra 82
Cassiculosphaeridia 141
  reticulata 141, **142,**; Pl. 3, fig. 7; Pl. 4, fig. 3
Castanopora 8, 12
  guascoi 8
  jurassica **7–8**, 11, 14, 19, 31, 37, 41, Pl. 7, figs. 4–7
Catenella 223
  opuntia 223
Cave Sandstone 293
Caytonidea 410, 424, 426
  faveolata 410, 411
  terraefullonicae **410–411**; Pl. 10, figs. 2, 7, 8; Pl. 11, figs. 1–3
Cellaria 9
  smithi 9
Cellepora 9
  complanata 29
  davaiacensis 9
  polythele 9
  ricata 30
  (*Dermatopora*) *faujasi* 8
  (*Discopora*) *subgranulata* 30
  koninckiana 6
Centrarchidae 92
Centroberyx affinis 68
Centropomidae 87, 92
Centropomus 87
Ceratocorys 136
  veligera 136
Chaetodon 87
Chaetodontidae 87, 92
Chañares Formation 281
Chanaria 281, 284
Channiformes 89, 93, 95, 96
Chanos 54
Chara knowltoni 214, 215
  medicaginula 217
Characeae 217
Charales 214, 217
Charixa vennensis 13
Cheilanthites gopperti 229
Cheilostomata 3, 4, 9, 12, 13, 14
Chelmo 87
Chinle Formation 290
Chlamydophorella 156
  nyei 155
Chlorophthalmus 81
Chlorophyceae 214
Chondrus crispus 223
Chouberticyathus 342
Chrysomonadinae ? 140
Chytroeisphaeridia **140**
  chytroeides 141
  euteiches 141; Pl. 3, figs. 8, 9
  sp. 141
Cichlidae 87
Circonitella 214–215
  knowltoni **215–216*–217**; Pl. 1, figs. 1–5
Circulodinium deflandrei 166
Cirrhitidae 87
Cirrhitus 87
Cisternifera 9
Cladocopida 427
Cladocopina 427
Cladograpsus capillaris 185
  linearis 185, 186
Cladophlebis albertsii 237
  browniana 238
  dunkeri 238
  longipennis 237, 238
  (*Klukia*) *dunkeri* 238
Claruscyathus 363
Cleistosphaeridium 152, 157
  ancoriferum 155
  armatum 110, **153–154**; Pl. 8, figs. 1, 2, 12
  heteracanthum **152**; Pl. 7, fig. 8
  huguonioti 109, **155–156**; Pl. 7, fig. 10
  var. *pertusum* **156–157**; Pl. 7, figs. 6, 7, 9
  multifurcatum 110, **152–153**; Pl. 8, figs. 7, 10
  polypes **154**, 155; Pl. 6, figs. 7, 8
  var. **clavulum 154–155**; Pl. 6, figs. 9, 10
  ? **aciculare 158**; Pl. 6, figs. 11, 12
  ? *flexuosum* **157**; Pl. 7, fig. 4
  ? **parvum 157–158**; Pl. 7, figs. 11, 12
Climacograptus 192
  minimus **191–193**; Pl. 4, fig. 3
  minutus 191*, 192*, **193–194**; Pl. 4, figs. 1, 2
  scalaris miserabilis 193; Pl. 4, fig. 2
  tangshanensis linearis 193
  spp. 188
Clonograptus 204
Clupavidae 86, 98
Clupavus 84, 85
Coilostega 13, 22
Cometodinium obscurum 137
Coniferales 211
Copleicyathus 344
  confertus 349
Coronifera **161**
  oceanica 161, **162**; Pl. 8, figs. 8, 11

Corynoides calicularis 195
Coscinocyathus 325, 329, 330, 369
  annulatus 337
  cellularis 330
  cribripora 340
  equivallum 326
  papillatus 334
  papillipora 338, 339
  petersi 331
  quadratus 328
  retifer 332
  rhyacoensis 329
  rugosus 325
  textilis 329
  unilinearis 330; Pl. 13, fig. 4
Coscinopleura 29
  lamourouxi 29
  sp. **29**, 41
Coscinoptycta 325, 330
  convoluta 330
Coscionteichus 325
Cribroperidinium 121, 124, **125**, 128
  edwardsi 127, 128
  intricatum 109, 110, **125–126*–127*–128**; Pl. 2, figs. 1–3
  muderongensis 127, 128
  orthoceras 121, 127, **128–129**, 134*
  sepimentum 125
Crisisina 17
  carinata **17**, 41; Pl. 1, figs. 4, 5
Cristivomer 84
Cryptograptus 194
  tricornis 191*, **194–195**; Pl. 4, figs. 4, 5, 6
    schaeferi 195
Cryptostomata 14
Ctenostomata 14
Ctenothrissa **54–56**, 63, 81, 83, 84, 86, 87, 93, 98, 99
  microcephala 55*
  radians 55
  signifer 54*, 55
  vexillifer 54
Ctenothrissidae 54, 83
Ctenothrissiformes 49, **50–51**, 83, 86, 98, 99
Cyathocricus 299, **318–319**, 369, 372
  annulispinosus 318, 320, 322, 369
  dentatus 318, 319, **321*–322**; Pl. 6, figs. 1–3
  tracheodentatus 318, **319–320***, 322; Pl. 5, figs. 4, 5; Pl. 6, fig. 4
Cycadales 210, 211, 242
Cyas 246
  revoluta 246, 248
Cyclocyathellidae 317
Cyclocyathus 318, 319, 372
Cyclonephelium **166**, 168, 171
  compactum 167
  distinctum **166–167**, 169*, 170; Pl. 11, figs. 6, 7, 8, 10
  eisenacki 166, 169*, **170–171**; Pl. 8, figs. 3, 4; Pl. 9, fig. 4
  membraniphorum 166, **167–168**; Pl. 11, fig. 9
  paucispinum 166, **170**; Pl. 9, figs. 1, 2
  vannophorum 166, **168**, 169*, **170**; Pl. 9, fig. 3 Pl. 11, figs. 11, 12
  attadalicum 168
Cyclostomata 9, 15
Cymatiosphaera cingulata 173
Cynidiognathus longiceps 291
Cynognathus Zone 257, 285, 290, 291, 292, 293
Cypridacea 384, 399
Cyrtograpsus murchisoni 202
Cyrtograptus centtrifugus 202, 203
  murchisoni **202**–203*, Pl. 5, figs 8, 9
  bohemicus 202
  crassiusculus 203
  rigidus 203
Cytheracea 385, 399
Cythere 394
  blakeana 393
  bradiana 390, 391
  corrosa **424**, 426 ; Pl. 13, fig. 4
  drupacea 393, 394, 427
  guembeliana 388, 412
  juglandice 389
    major 389, 412
    minor 395
  monticula 431
  oscillum 412, 413; Pl. 12, fig. 2
  schwageriana 387; Pl. 2, fig. 6.
  speciosa 395
  sphaerulata 411
  subconcentrica 392
  ? *tenella* **394**; Pl. 5, fig. 8
  trapezioides 395
  walfordiana 395
  (*Cythereis*) *quadrilatera* 394
Cythereis 394
  blanda 394
  cf. *blanda* **394**; Pl. 5, figs. 3, 7
  fullonica 401
  walfordiana 395
Cytherella 380, 381, 395
  catenulata 396
  fullonica **395**; Pl. 5, fig. 9; Pl. 6, fig. 1
  jugosa 381
  subovate 380, 381
  suprajurassica 381
  symmetrica **380–381**; Pl. 1, figs. 1, 2
Cytherellidae 380, 395
Cytherelloidea 381, 396
  catenulata **396**; Pl. 6, figs. 2, 3
  eastfieldensis 382
  jugosa **381–382***; Pl. 1, figs. 3, 4
  paraweberi 382*
  refecta **396–397**; Pl. 6, figs 4–7
  weberi 382
Cytheridae acutiplicata 416
  aequabilis **424**; Pl. 13, fig. 3

bicarinata 395, 420, 421
blakeana 393, 423
bradiana 391*, 418
coarctata **424**; Pl. 13, fig. 5
craticula 390, 391*, 392, 418; Pl. 4, figs. 2, 3
dolabra 406, 407, 408
egregia 393, 395
eminula **425**; Pl. 13, fig. 6
eximia 395
fulgarata 419
horatiana 402
ignobilis 407, 408, 409; Pl. 9, fig. 8
limaciformis 422
obovata 404
ostreata 420
parallela 407, 408; Pl. 9, fig. 3; Pl. 10, fig. 1
pentagonalis 407, 408; Pl. 9, figs. 2, 6
persica 415
politula 395
pulvinar 388, 412; Pl. 4, fig. 1
punctiputeolata 409, **425**; Pl. 13, fig. 8
pura 395
puteolata 407, 408; Pl. 9, fig. 5
refecta 396
renoides 395
retorrida 394, **425*–426***; Pl. 15, fig. 3
rugifera 395
sedata 395
spinifastigiata **426**; Pl. 13, fig. 7
spinigyrata **426–427**; Pl. 13, fig. 9
striblita 412, 413; Pl. 5, fig. 2
subeminula 395
subperforata 385; Pl. 2, fig. 4
subtrigona 405
sugillata 409
terraefullonicae 410
transversiplicata 393, 423
trapezoidalis 388, 412
ventrosa 395
visceralis 399
vulsa 400
winwoodiana 395
Cytherideidae 406
Cytherideinae 406
Cytheropteron jonesanum 393, 394
Cytherura 434
  bathonica 434; Pl. 16, figs. 5–8
  ? *liesbergensis* 435
  mediojurassica 434–435; Pl. 15, fig. 6; Pl. 16, figs. 1, 2
  striata 434
Cytheruridae 393, 431
Cyttus 96

Dactylopteriformes 96
Daptocephalus 286
Decurtaria 37
  allecta 38
  cornuta 37, 38
  cf. *cornuta* **37–38**, 41; Pl. 7, figs. 1, 2
Deflandrea 110
Dendrocyathus 354
Dendrograptus lentus 204
Dermogenys 90
Description of sections
  Compton Bay, Isle of Wight 112, 113*
  Devon 115, 117*
  Escalles Borehole, Pas de Calais 115, 118*
  Fetcham Mill, Surrey 111*, 112
  Hunstanton, Norfolk 115, 116*
  Saskatchewan 115, 119*
  Speeton, Yorkshire 112, 114*
  Texas 115
Diademodon 259, 292
  polyphagus 292
  rhodesiensid 292
Diastopora 9
  lamellosa 5
  ranvilliana 9
Dicellograpsus elegans 187
  moffatensis 189
Dicellograptus 188, 190
  anceps 189
  duvaricatus 189, 190
  elegans **187–188***, 190; Pl. 3, fig. 1
  moffatensis 188*, **189–190**; Pl. 3, figs. 5, 6
    alabamensis 190
  morrisii 188, 190
  pumilus 188
  vagus 190
Dicentrarchus 87
Dichopteris delicatula 236
  sp. cf. *D. laevigata* 240
Dicranograptus 190, 191
  brevicaulis 190
  clingani **190–191***; Pl. 3, figs. 2, 3, 4
Dictyocyathidae **342**, 344
Dictyocyathus 342, 344, 370
  annularis 305
  graphicus 346, 348
Dictyophyllum roemeri 228
Dictyopyxidia 141
Didymograpsus elegans 187
Didymograpsus moffatensis 189
Dimorphostylus 32, 33
  tetrastichus 32, 33
Dinanomodon 286
Diniferophycidae 120
Dinodontosaurus 281, 284
  turpior 283, 284
Dinophyceae 120
Dinopterygidae 62, **66**–67, 92, 98
Dinopterygoidei **62**, 86, 87, 88, 97, 99
Dinopteryx 67, 68, 84, 87, 88, 93, 95, 99
  spinosus 66
Diphyes 161
Diplograpsus foliaceus 194
  minimus 191, 192*, 193

  minutus 192, 193
  pristis 192, 193
  tricornis 194
Diplograptidae 194
Diplopholeos 27
Dipteridaceae 228
Diretmidae 68, 88, 99
Diretmus 68, 88, 99
Diversograptus ? capillaris **198**, **199***, **200**
Doidyx 142
Dokidocyathidae 305, 372
Dokidocyathus 305
Drepane 87

Esienackia crassitabulata 136
Ektyphocythere 430
  parva **430**; Pl. 14, figs. 1, 3
Ellipsoidictyum 141
  cinctum 141
Ellipsodinium **129–130**
  rugulosum **130**, 139*; Pl. 3, fig. 1
Eops 54, 63, 83, 84, 85, 86, 88, 98
Emydops 285
Endothiodon Zone 258
Entalophora 9, 16
  benedeniana **16**, 41
  madreporacea var. *benedeni* 16
Eocytheridea 406
  faveolata 406
  sp. **406**; Pl. 8, fig. 1
Epelidosphaeridia **142**
  spinosa **143**; Pl. 3, figs. 10–12
Ephippidae 87, 98
Ephippus 87
Equisetales 211, 227
Equisetites **227–228**
  lyelli 227
Er-ma-ying Formation 290
Erismacoscinidae **325**
Erismacoscinus **325**, 332, 369
  cancellatus 332
  cellularis **330–331**; Pl. 8, figs. 1, 4
  equivallum **326–327**, 328, 331; Pl. 7, figs. 1–3, 5
  marocanus 325
  papillatus 334
  petersi **331–332**, 333; Pl. 10, figs. 4, 5
  quadratus **328–329**; Pl. 7, fig. 4; Pl. 8, fig. 5
  retifer **332–333**; Pl. 10, figs. 2, 3
  rugosus **325–326**, 328, 331; Pl. 8, figs. 2, 3
  textilis **329–330**; Pl. 9, figs. 1–4
  (*Pluralicoscinus*) 325
Erythrosuchus 291
Escarpment Grit 258, 293
Escharidae 9
Eschara 9, 24
  bellona 35
  caecilia 36
  cepha 34
  gaimardi 24
  nysti 34
  oblita 40
  ranvilliana 9
  striata 39
Escharifora flabellata 40
Escharinella simplex 30
Ethmocoscinus **338–339**, 369
  papillipora **339**; Pl. 3, fig. 3
Ethmocyathidae 299, **322–323**, 372
Ethmocyathus 322, **323**, 369, 372
  lineatus **323–324***; Pl. 5, figs. 1–3
Ethmophyllidae 317
Ethmophyllum 313, 314, 370
  dentatum 318, 319, 321
  flexum 315, 316
  poletevae 315
  vermiculatum 315
Euparkeria 291
Exellia 97, 98, 100
Exochosphaeridium 131, **162**, 166
  " *hirsutum* " group 164, 165
  phragmites **163**; Pl. 7, fig. 5
  pseudohystrichodinium **163–164**; Pl. 11, figs. 4, 5
  spinosum 166
    var. *deflandrei* 165, 166
  striolatum 162, 163, **164**, 165
    var. **truncatum** 110, **164–166**; Pl. 7, figs. 1–3
  (*Hystrichosphaeridium*) cf. *hirsutum* 165

Fastigatocythere 389, 412
  juglandica **389**, **412**; Pl. 3, figs. 4, 7, 8; Pl. 12, fig. 3
Filicales 228
Flindersicyathidae **344**, 372
Flindersicyathus **344–346**, 350, 370, 371, 372
  (*Flindersicyathus*) 344, 345, 348, 349, 370, 371, 372
  circliporus 346
  contractus 346
  decipiens 344, 348
  graphicus **346–347*–348**, 363; Pl. 12, figs. 3, 4, 5
  irregularis 346, **348–349**; Pl. 14, fig. 4
  latiloculatus 346
  macdonnelli 346
  major 346, **349–350**; Pl. 14, fig. 2
  multifidus 346
  rete 346, 348
  simplex 346
  speciosus 346, **350**; Pl. 14, figs. 1, 3
  tabulatus 346
  (*Pycnoidocyathus*) 344, 345, **350–351**, 352, 354, 370, 371, 372
  maximipora 346, **352–353**; Pl. 15, fig. 3
  parvulus 346
  ptychophragma 346
  simplex **352**; Pl. 15, fig. 2
  synapticulosus 346, 350, **351**; Pl. 15, fig. 1
  vicinisepta 346, **353–354**; Pl. 15, fig. 4
Floridina 31

Floridinella 31
  scutata 31; Pl. 4, fig. 7
" Flustra " flabelliformis **4–5**
Flustrella 20
  baculina 20
  convexa 25, 26
  irregularis 21
  marginata 25
  simplex 19
Flustrellaria incrassata 23
Fromeaceae 140
Fromea **140**
  amphora **140**; Pl. 3, figs. 2, 3
Frurionella 38, 39
  europaea 39; Pl. 8, fig. 8
  fertilis 3, 11, **38–39**, 41; Pl. 8, figs. 5–7

Gabrielsocyathus 363
  deasensis 364
  gabrielsensis 364
  poolensis 364
Gasterosteiformes 96
Gaterin 87
Geniculicyathus 325
Gephyroberyx 68
Gesoriacula 431
Gibberichthyidae 68, 96
Gibberichthys 68
Ginkgoales 210, 211, 248
Gleichenites cycadina 238
Glossograptus 194
Glyptocythere 388, 389, 412
  costata 416
  guembeliana **388–389**, **412**, 416; Pl. 3, figs. 1, 2; Pl. 4, fig. 1
  juglandica 389
  oscillum **412–415** [414*]; Pl. 5, fig. 2; Pl. 12, fig. 2
  persica **415*–416**; Pl. 12, fig. 1
  rudimenta 413, 414*, 415
  tuberodentina 416
Gnathoberyx **74–75**
  stigmosus 74
Gonyaulacysta 120, 121, 125, 128, 132
  ambigua 124
  cf. *ambigua* 120
  apionis 127, 128
  cassidata **120**
  delicata 123*–124; Pl. 1, figs. 7, 8
  diaphinis 127, 128
  edwardsi 125
  exilicristata 110, **121**, 122*, 125; Pl. 1, figs. 1, 2
  fetchamensis **120–121**
  muderongensis 125
  obscura 128
  orthoceras 125
  wetzeli 128
  whitei **120**
  Sp. A. 122*, **124–5**; Pl. 1, figs. 9, 10
Gonyaulacystaceae 120
Gonyaulax 125
  edwardsi 128
  helicoidea subsp. *cassidata* 120
  muderongensis 128
  orthoceras 109, 128
  sp. 110, 127
Grammascosoecia 19
  dichotoma 19
Grammicolepidae 96
Graptolithus becki 195
  clingani 195
  hisingeri 197
  intermedius 196
  millepeda 195
  nilssoni 197
  tenuis 197
Gymnospermae 242
Gyrogona 217
  medicaginula **217–218**

Hadrocytheridea 379, **406**
  dolabra **407–409** [408*], 425; Pl. 9, figs. 1–8; Pl. 10, fig. 1
Hagenowinella 23
  cf. *incrassata* **23–24**, 41; Pl. 2, figs. 1–3
Hausmannia 228
  dichotoma **228**; Pl. 3, figs. 1, 2
  pelletieri 228
Hekistocythere 379, **428**, 430
  venosa 428–429*–430; Pl. 14, figs. 2, 4, 9; Pl. 15, fig. 7
Heliodinium voigti 175
Heniochus 87
Hepaticae **218–219**
Hepaticites 219, 220, 221
  amauros 223
  arcuatus 220
  haiburnensis 220
  laevis 220
  langi 224
  rosenkrantzi 223
  ruffordi 220, 223; Pl. 2, figs. 4, 5
  zeilleri **219–220**, 223; Pl. 2, figs. 1–3
Heterocella 27
Heterocrisina 16
  abbottii 16
  communis **16–17**, 41
Heteropora reticulata 18
Hexasphaera asymmetrica 152
Hiodon 84
Hippothoa 9
  simplex 13
Histiocysta 138
  palla 138–139*–140; Pl. 1, figs. 5, 6
Histiopterus 87
Holocentridae 67, 68, **75–76**, 77, 88, 94, 95, 99
Holocentrus 68, 75, 76

  ascensionis, 68, 76
Homocytheridea 424
Homonotichthys **60–61**, 88, 94, 95, 99
  dorsalis 60, 61
  pulchellus 60*, 61
  rotundus 61
Hoplopteryx **69–72**, 73, 75, 94, 95
  antiquus 70
  gephyrognathus 70, 71
  lewesiensis 70*, 71*, 72
  lewisi 71
  macracanthus 70, 71
  simus 70, 71
  spinulosus 71
  syriacus 71, 72
  Hoplostethus 68, 70, 72, 74, 75, 94
  mediterraneus 67*, 68, 69
Howesia 291
Hymenopteris psilotoides 238
Hynnis 98
Hystrichodinium 175
  dasys **175–176**; Pl. 10, figs. 8, 9
  pulchrum 109
  voigti 109, **175**; Pl. 10, figs. 6, 10
Hystrichokolpoma 159
  ferox **159–160**; Pl. 9, figs. 5, 6, 7
Hystrichosphaeraceae 172
Hystrichosphaera 110, 172
  cingulata var. *cingulata* **173**
    var. *perforata* 173
    var. *polygonalis* 174
    var. *recticulata* **173**–174
  crassimurata **174**
  crassipellis **174**
  furcata 172, 173
  ramosa var. *gracilis* **172**
    var. *multibrevis* **173**; Pl. 10, figs. 3, 4
    var. *ramosa* **172**; Pl. 10, figs. 1, 2, 5
    var. *reticulata* **173**
  cf. *ramosa* 174
Hystrichosphaeridiaceae 143
Hystrichosphaeridium 143
  ancoriferum 155
  anthophorum 147
  armatum 153
  asterigerum 110
  asymmetricum 152
  bowerbanki **145**; Pl. 5, fig. 9
  complex 146
  costatum 146
  deanei **144**; Pl. 4, fig. 1
  difficile **145–146**; Pl. 4, figs. 2, 6, 7
  ferox 159
  heteracanthum 152
  hirsutum 165
  huguonioti 155
  longifurcatum 110, 158
  mantelli 109, **145**; Pl. 4, fig. 9
  multifurcatum 152, 153
  parvispinum 161
  polytrichum 110
  pseudohystrichodinium 163
  radiculatum **144–145**; Pl. 4, fig. 8
  readei **144**
  recurvatum 151, 154
    subsp. *polypes* 154
  reniforme 148
  cf. *salpingophorum* 109
  siphoniphorum 148
  spinosum var. *deflandrei* 166
  stellatum 144
  cf. *striolatum* 110
  tubiferum **143–144**; Pl. 5, figs. 5, 8
  sp. **22**. 110
  sp. **23**. 111

Ichthyodectes 84
Idmidronea 16
  macilenta **16**, 41
Idmonea abbottii 16
  communis 16
  disticha 16
  lichenoides 18
  macilenta 16
  pseudodisticha 16
  ramosa 16
  (*Tubigera*) *antiqua* 16
Irregularia 342, 370
Ischigualastia 257, 285, 290
Ischigualasto Formation 290

Kannemeyeria 285, 290, 291, 292
Kannemeyeriidae 290
Kansius sternbergi 78
Kawinga Formation 293
Kingori Sandstone 293
Kinkelinella 430
  tenuicostati 430
Kirtonellinae 430
Kistecephalus Zone 258, 285, 286, 293
Korojonia dubiosa 109
Korsogasteridae 68
Kuhliidae 87
Kuhlia 87, 91
Kyphosus 87
Kyphosidae 87, 92

Labiostomella 14
Lampridae 98
Lampridiformes 49, 78, 81, 96, 97, 98, 100
Lampridoidei **78**, 97
Lampris 78, 81, 97
Lateolabrax 87
Leckenbya valdensis 238
Lepidorbitoides 10
Leptograptus 185, 187
  capillaris **185–186**; Pl. 1, figs. 1, 2
  flaccidus 186

  arcuatus 186
Leptolepis 84, 91, 98
  coryphaenoides 85
  dubia 85
  normandica 85
Leptosomus 82
Lethrinidae 87
Lethrinus 87
Lingulodinium 165
Lissoberyx 72, 73, 75, 94, 95
  dayi 72*
Litosphaeridium 148
  siphoniphorum **148–149*–150**; Pl. 6, figs. 3, 4
Lobotes 87
Lobotidae 87
Loculicyathus (*Loculicyathus*) 310, 372
Loculicyathus (**Loculicyathellus**) 299, **310**, 372
  floreus **310–311**; Pl. 3, figs. 1, 2, 4
Lonchopteris mantelli 239
Looneyella **431**
  monticula 431; Pl. 14, fig. 6
  quadrispina 431
  subtilis **431–432**; Pl. 14, figs, 7, 8
Lophocythere **389–390**, 416; 417, 418, 421
  acutiplicata **416–417**; Pl. 1, fig. 8; Pl. 12, figs. 4, 6
  bradiana **390–391*–392**, 416, 417, **418**; Pl. 3, figs, 3, 5, 6; Pl. 4, figs. 2, 3, 4
  fulgurata **419–420**; Pl. 12, fig. 7
  multicostata 392
  ostreata 390, 419, **420–421***; Pl. 12, fig. 5
  scabra 421
  septicostata 391, **418**; Pl. 12, fig. 8
  sp. **418*–419**
Lower Cambrian archaeocyathid Stratigraphy 368–371, 372
  Australia 368, 369, 370, 371
  Morocco 369
  Sardinia 369, 370
  Siberian platform 368, 369, 370
  Southern Siberia 368, 369, 370
Luangwa drysdalli 259, 292
Luciocephalus 89
Lunulites 34
  sp. 11, **34**, 41
Lutjanidae 87
Lutjanus 87
Lycopodiales 224
Lystrosaurus 285
Lystrosaurus Zone 285, 291, 293

Macristiella perlucens 51
Macristiidae 51
Macristium 50
  chavesi 50
Macrocypris bradiana 385; Pl. 2, fig. 3
  horatiana 399; Pl. 7, fig. 2
  terraefullonica 399
Madumabisa Mudstone 293
Malacostega 13, 21, 22
Manda Formation 290, 291, 292, 293
Marchantiales 218, 220
Marchantiolites 219
Marchantites 218, 219, 220
  hallei 220
  zeilleri 219
Matoniaceae 228
Matonidium 228
  goepperti **228**
Medialuna 87
Melamphaeidae 68
Melamphaes 68
Membranilarnax cf. *pterospermoides* 140
Membranipora 14, 19
  bipunctata 8
  constricta 13; Pl. 7, fig. 8
  elliptica 13
  fragilis 13
  genucia 19, 20
  jurassica 3, 4, 6, 7
  neocomiensis 13
  ? *obliqua* 13
  simplex 20
  unipora 11, **19–20**, 41; Pl. 2, figs. 7, 8
Membraniporae 13, 20
Mene 80, 81, 97, 98, 100
  maculata 80*, 81
  oblongus 80
  phosphaticus 97
  rhombeus 80
Menidae 80, 100
Mesosuchus 291
Metacoscinidae **363**, 367
Metacoscinus **363–364**, 370
  insigne 364
  reteseptatus 363, **364–366**; Pl. 17, figs. 1–4
Metacyathidae **354**
Metacyathus 299, 355, 356
  irregularis 355, 359
  taylori 355, 360
Metacytheropteron 393, 427
  drupaceum **393–394**; Pl. 5, figs. 4–6
  sp. 393
Metafungia 354, 358, **361–362**, 370
  reticulata 361, **362–363**; Pl. 18, figs. 1–3
Metaldetes 299, 348, 354, **355–356**, **358**, 370
  columbianus 356
  conicus 358, 359
  cylindricus 355, 356
  dissepimentalis 356, **358–359**, 361; Pl. 16, figs. 1–3
  dissutus 356
  graphica 346, 348
  irregularis 356, **359–360**, 361; Pl. 16, fig. 4
  proteus 356, 358
  ramulosus 356
  solidus 356
  spiralis 358

  superbus 358
  taylori 358, **360–361**; Pl. 13, figs. 1–3
Micrhystridium ambiguum 109
  veligerum 136
  sp. ? 138, 140
Microdiniaceae 132
Microdinium **132**, 135, 136, 137
  ? *crinitum* **137**; Pl. 2, figs. 7, 8
  distinctum 133, 134*, **135**; Pl. 2, figs. 9–11
  echinatum 133
  irregulare 136
  ornatum 132, 133
  cf. *ornatum* **132–133**, 134*; Pl. 4, fig. 5
  setosum **133**, 134*; Pl. 2, fig. 4
  variospinum 134*, **135**; Pl. 2, figs. 5, 6
  veligerum **136–137**; Pl. 3, fig. 4; Pl. 4, fig. 4
Micropneumatocythere 392, 422
  limaciformis **422–423**; Pl. 13, fig. 1
  quadrata 422, 423
  subconcentrica **392**; Pl. 4, fig. 7
Micropora 32, 33
  rugica 32, 33
  subgranulata 30
  transversa **32–33**, 41; Pl. 7, figs. 9–12
Microporidae 13, 33
Mohria 232
Molteno Beds 291, 293
Monocentridae 68, 69, 95, 96
Monocentris 63, 68, 69, 87, 88, 89, 99
  japonicus 69*
Monoceratina 399, 400
  ungulina 400
  visceralis **399–400**; Pl. 7, fig. 3
  vulsa **400–401**; Pl. 7, fig. 5
Monocyathida 302
Monocyathidae 302
Monocyathus **302–303**, 305, 369
  absolutus 302
  bilateralis 302
  contractus 302
  copulatus 302
  kuzneskii 302
  lebedevae 302
  irregularis 304
  macrospinosus 302
  mellifer **302–304**; Pl. 1, fig. 4
  nalivkini 302, 303
  operculatus 302
  partibus 303
  polaris 303
  porosus 302, **303**; Pl. 1, fig. 3
  robustus 303
  sibiricus 303
  simplex 303
  sparsipora 303
  spinosus 303
  tenuimurus 303
  tolli 303
  unimurus 303
Monodactylidae 87, 92
Monodactylus 87
Monograptus 198
  attenuatus 198, 200
  capillaris 198
  clingani **195–196**; Pl. 5, figs. 1–5
  communis 197
  gemmatus 198, 199*, 200
  intermedius **196*–198**; Pl. 5, fig. 6
  involutus 197
  spiralis 203
  sp. (*atavus* or *acinaces* type) 192
  (*Rastrites*) *gemmatus* 198
Morone 87
Mugil 88, 92
Multicavea 19
Multicrescis 18, 19
  laxata 7, 11, 14, **18–19**, 31, 41; Pl. 1, figs. 6–8
Musci 218
Myctophidae 83, 99
Myctophoidei 49, 50, **81–83**, 86, 88, 98, 99
Myctophum 81
Myodocopida 427
Myosaurus 285
Myripristis 68, 75, 76, 77
  adustus 75*

Naiadita lanceolate 218
Nandidae 89, 93
Nathorstia valdensis 238
Nemagrapsus capillaris 185
Nematonotus 63, 68, 82, 83, 84, 85, 86, 88, 93, 98
  bottae 82*, 83
  longispinus 82*
Nemipteridae 87
Nemipterus 87
Neocyttus 96
Neomiodon 221
Neoscopelus 81
Neothunnus 89
Nilssonia 242, 244
  revoluta 244
  schaumburgensis 237*, **242–243*–244**
Nitella 215, 217
  flexilis 217
  hyalina 217
  polygyra 217
Nitellaceae 217
Nitellites 214
  sahnii 217
  sp.
Ntawere Formation 257, 258, 259, 262, 283, 284, 286, 290, 292, 293

Okulitchicyathus 354
Oligocythereis 401
  fullonica **401–402**; Pl. 7, fig. 6
Oligosphaeridium 146
  anthophorum **147–148**; Pl. 5, figs. 1–3

complex 110, **146–147**; Pl. 5, figs. 6, 7
perforatum 148
prolixispinosum **147**; Pl. 5, fig. 4
pulcherrimum 148
reniforme **148**; Pl. 6, fig. 1
reticulatum **147**
Omosoma **58–59**, 92
intermedium 58
pulchellum 58
sahelalmae 58
Omphalocyclus 10
Oncorhynchus 92
Onoclea sensibilis 235
Onychiopsis 219, 238
elongata 238
mantelli 238, 239
psilotoides 211, **238–239**
Onychocella 4, 5, 12, 34
bathonica 3, 4, **5–6**, 7, 15, 25, 41
bellona 11, **35–36**, 41; Pl. 6, figs. 5–7
cf. *cepha* 11, **34–35**, 41; Pl. 6, figs. 1, 2
flabelliformis 6
hagenowi 6
koninckiana 6
lamarcki 35
nysti **34,** 41; Pl. 6, figs. 3, 4
piriformis 5, 6, 11, 41; Pl. 5, figs. 11, 12
Onychocellaria 36
caecilia 11, **36–37**, 41; Pl. 5, figs. 1–6
Onychocellidae 13
Orbicyathus 346
Orbitoides 10
Oreosomatidae 96
Orthograptus cf. *whitfieldi* 189
Orthonotacythere 432
nodosa 432
pulchella 432
sp. **432**; Pl. 15, fig. 1
Osculipora 17
truncata **17**, 41

Pachycormidae 98
Pachypeteris 240
lancsolata **240–241*–242**; Pl. 1, fig. 6
Pagruo 87
Palaeocentrotus 81, 97
Palaehystrichophora infusorioides 109
cf. *paucisetosa* 109
Palaeoperidinium castanea 131
spinosum 142, 143
ventriosum 130, 131
Palaeostomocystis echinulata 157
Paleschara 13, 14
Paleschuridae 13
Paracoscinus 363, 364
Paracycas cteis 246
Paracyclotosaurus 292
Paracyprididae 385, 399
Paracypris 399
terraefullonicae **399**; Pl. 7, figs. 2, 4
Paracytheridea 433
blakei 433; Pl. 15, figs. 4, 5, 9, 10
caytonensis 433
Parakannemeyeria 285, 290
Paranacyathus 312, 354
magnipora 311
Parariscus 433
bathonicus **433**; Pl. 15, figs. 2, 8
Parasudis 81
Paratrachichthys 68
Pareodiniaceae 130
Pareodina sp. 109
Parupeneus 91
Pateroperca **51–52**, 53, 54, 55, 83, 84, 86, 87, 93, 98
libanica 51*****, 52, 53
Pavobeisselina 40
Pecopteris reticulata 239
Pegasiformes 96
Pelletieria 232
valdensis **232–233*–234*–235**; Pl. 6, figs. 1, 2
Pellia 220
Peltostega 291
Pentaceropsis 91
recurvirostris 91*****, 92
Pentacerotidae 87, 91
Percichthyidae 87, 89, 92
Percidae 87
Perciformes 49, 87, 88, 92, 93, 95, 96, 99
Percoidei 86, 89, 92, 96
Permo-Trias continental sediments classification-Africa 293
Petalopora sp. **18**, 41; Pl. 1, figs. 1–3
Pharmacichthyidae **63–65**, 92, 97, 100
Pharmacichthys 49, 63, 65, 66, 84, 87, 88, 93, 94, 95, 97, 98, 99
venenifer 63
Pinacocyathus **342**
spicularis 342, **343*–344**; Pl. 12, figs. 1, 2
Placerias 290
Platax 87
Platycopina 380, 395
Platycythere 431
verriculata **431**
sp. **431**; Pl. 14, fig. 5
Plecoglossus 86
Pleurograpsus linearis 186
Pleurograptus linearis **186–187***; Pl. 2, figs. 1–3
linearis simplex 186, 187
Pleuronectes 89
Pleuronectiformes 93, 95
Pleuronectoidei 89
Pliophloea 37
gluma 37
sp. 7, 14, 15, **37**, 41; Pl. 7, fig. 3
Pithodella 24
Podocopida 380, 395
Podocopina 383, 397
Polycope 427

  fungosa **427–428**; Pl. 16, figs. 4, 9
Polycopodae 427
Polycoscinidae **334**
Polycoscinus 334, 369
Polydactylus 87
Polymixia 56, 57, 58, 59, 60, 61, 88, 94, 95
  japonicus 57
  nobilis 56*, 57
Polymixiidae **56–57**, 61, 92, 93, 95, 98
Polymixioidei 49, 56, 63, 66, 84, 86, 88, 99
Polynemoidei 87
"*Polyphyma bulbosa*" 12
Polypodiaceae 235
Polyprion 87
Polysphaeridium 151
  laminaspinosum **151**; Pl. 4, figs. 10, 11
  pumilum **151**
Polystichum 235, 236
Polystillicidocyathus 318, 327
Pomacanthus 87
Pomadasyidae 87
Pomatomidae 87
Pomatomus 87
Pontocyprella 385
  harrisiana 379, **385**; Pl. 2, fig. 3
Porina 13
  cenomana 13
  flabellata 40
Porinidae 13
Praechara symmetrica 215
Praeschuleridea 387, 405
  schwageriana **387**; Pl. 2, fig. 6
  subtrigona intermedia 387
  magna 405
  subtrigona 387, **405**; Pl. 8, figs. 4–6
  sp. **388**; Pl. 2, fig. 8
Pristolepis 89
Procytheridea 430
  minuta 430
  parva 430
Progonocythere 389, 423
  blakeana 393
  juglandica 389
  stilla **423**; Pl. 13, fig. 2
Progonocytheridae 388, 409, 428
Progonocytherinae 388, 409
Prolates 88
Prolixosphaeridium **160**, 161
  conulum **160–161**; Pl 8, figs. 5, 6
  granulosum 161
  mixtispinosum 161
Prosoporella 37
  cornuta 37
Protocheilostomata 14
Protocytheridae 430
Protopharetra 348, 354, 356, 370
  graphica 346, 348
Psettodes 89
Pseudoceratium turneri 171
Pseudocycas dunkeriana 212
Pseudotorellia **248**, 250
  angustifolia 249
  crassifolia 249
  ensiformis 249, 250
  ephela 249, 250, 251
  grojecensis 249, 251
  heterophylla **248–250*–251**; Pl. 6, figs. 6, 7
  longifolia 249
  minuta 249, 250, 251
  nordenskioldi 248, 249, 250
Pteridophyta 210, 211, 224
Pteridospermae 210, 211, 240
Pterophyllum schaumburgense 242
Puesto Viejo Formation 290
Puncturiella 33
  cf. *superba* **33–34**, 41; Pl. 4, figs. 8–10
Pustulopora benedeniana 16
Pycnoidocoscinus 363, **367**, 368
  pycnoideum **367–368**; Pl. 18, figs. 4–8
Pycnosterinx **59–60**, 99
  discoides 59
  dubius 59, 60, 61, 88
  gracilis 59
  latus 59, 60
  russeggerii 59*, 60
Pycnosteroides 65, 66, 67, 68, 84, 87, 88, 93, 95, 99
  levispinosus 65, 66*
Pycnosteroididae **65–66**, 92, 98
Pyripora texana 13

Quadricellaria 29
  elegans **29**, 41; Pl. 6, figs. 8–10
  excavata 29
  pulchella 29

Radulopora 3, **21–22**
  minor 3, 21, **22–23**, 31, 41; Pl. 3, figs. 6–10
  radula 21, 22*; Pl. 3, figs. 11, 12
Rastrites 198
  capillaris 198, 199*
  carnicus 201
  distans 200
  gemmatus 198
  linnaei 200, 201*
  maximus 184, 199, **200–201*–202**; Pl. 5, fig. 7
  cf. *peregrinus* 200
  spina 199
Rectocythere 409
  lincolnensis 410
  rugosa 409
  sugillata **409–410**; Pl. 10, figs. 3–6
Rectonychocella 27
Red Marl (Beds) 258, 259, 292, 293
Regularia 302, 312, 346, 370
Repteschärinella 29, 30
Retecava abbottii 16
  lichenoides 18
  ramosa 16

Retecoscinus 325, 367
Retepora lichenoides 18
truncata 17
Reteporidae 18
lichenoides 15, **18**, 41
Reticrisina 12
" *Reticulipora dianthus* " 12
Retropinna 86
Rhabdocnema 302
Rhabdocyathus 302, 304
tubexternus 304
Rhabdolynthus 302
Rhagasostoma bellona 35
simplex 30
Rhammatopora gaultina 13
(?) *johnstoniana* 13
pembrokiae 13
vinei 13
Rhiniopora 8
jurassica 7
scabra 7, 8
Rhytidosteus 291
Robustocyathidae 311
Robustocyathus **311**, 312, 369
argentus 311
annulatus 311
artecaveatus 311
biohermicus 311
densus 311
hupei 311
levigatus 311
magnipora **311–312**; Pl. 3, fig. 5
moori 311
novus 311
polyseptatus 311
proskurjakowi 311
pseudotichus 311, 314
salebrosus 311
spinosus 311
stapipora 309
subacutus 311, **312–313*–314**, 369; Pl. 3, figs. 6, 7
sucharichensis 311
tenuis 311
Rosseliana 31
thomasi 3, 7, 11, 14, 19, **31**, 41; Pl. 4, figs. 4–6
Ruffordia 229
goepperti **229–230*–231–232**; Pl. 4, figs. 1–7; Pl. 5, figs. 1–4
var. *latifolia* 229

Sajanocyathus 369
Salairocyathidae 332, 333, **336**
Salairocyathus **336**
(*Polystillicidocyathus*) 336
erbosimilis 336
(*Salairocyathus*) 336
annulatus 336, **337*–338**, 369, 372; Pl. 11, fig. 4
pospelovi 336
zenkovae 336
Salmo 84
Salmoniformes 81
Sangusaurus 285, **286**, 289, 290, 292
Sangusaurus edentatus 257, **286–287*–288*–289*–290**
Santa Maria Formation 281, 283, 284, 290
Sardinioides 82, 83, 98
attenuatus 83, 98
Saurida 81, 89
Scalenodontoides 291
Schedophilus 87
Schizaeaceae 229, 231, 232, 235
Schuleridea 385, 402, 403
(*Eoschuleridea*) 402
bathonica 386, 387, 403
horatiana **402–404**. [403*]; Pl. 7, fig. 7
subperforata **386**; Pl. 2, fig. 4
trigonalis **386–387**, 388; Pl. 2, fig. 7
(*Schuleridea*) *jonesiana* 379, 385; Pl. 2, fig. 5
Schulerideidae 385, 402
Schulerideinae 385, 402
Sciaena 87
Sciaenidae 87
Scolopsis 87
Scorpaemiformes 95, 96
Scorpididae 92
Selaginella **224**, 227
dawsoni **224–225–226*–227**
dichotoma 227
emmeliana 227
hallei 224, 227
sanguinolenta 227
Selaginellaceae 224
Selaginellites 224
dawsoni 224
nosikovii 227
polaris 227
Selene 98
Semieschara complanata 31
Semiescharinella 29, 30
complanata 11, **29–30**, 41; Pl. 4, figs. 11–15
Semiescharipora cornuta 37
Semiophorus 97
Serranidae 87, 92
Sertulariadae 192
Siderolites 10
Siniperca 63, 89
chuatsi 90*
Sinokannemeyeria 285, 290
Siphonella elegans 20
Smittipora 27
Soleoidei 89
Sparidae 87
Sparus 87
Spermatophyta 240
Sphaerodon 87
Sphenocephalidae **61–62**, 92, 98
Sphenocephalus 92, 93, 94, 95, 99

  fissicaudus 61, 62*
  kurriana 212
  sternbergiana 212
Sphenopteris fittoni 238
  fontainei 238
  mantelli 238
  ruffordi 238
Sphyraena 87, 88, 92
Sphyraenoidei 87
Spinosocyathus 342
Spirillicyathus 344
Spirocyathella 344
Spirocyathus atlanticus 348
  irregularis 344, 348
  major 349
  speciosus 350
Spirograptus 197
  intermedius 197
  planus 197
Stahleckeria 257, 282, 283, 284
  potens 282*
Stahleckeriidae 281
Stamenocella 25
  inferaviculifera 25
  marginata 6, 11, **25–26**, 41; Pl. 3, figs. 1–5
  mediaviculifera 25
Stephanoberycoidei 68
Stichocentrus **77–78**, 94, 95
  liratus 77, 78*
Stichopora regularis 16
Stillicidocyathidae 317, 319
Stillicidocyathus 318
Stromateoidei 87
Stomatopora smithi 9
Surculosphaeridium 110, 158
  longifurcatum **158**–159; Pl. 8, fig. 9
Synbranchiformes 96
Synodontidae 82
Synodus 81
  foetens 57
Syringocnema 301, 370, 371

Tabellaecyathidae 370
Tabellaecyathus 348
Taeniopteris beyrichii var. *superba* 244
Teilhardia valdensis 238
Tannuolacyathidae 325
Tannuolacyathus 325
Tanyosphaeridium 151, 160
  variecalamum **151**; Pl. 6, figs. 2, 5
Tarpon 54, 84, 85
Terquemula 393, 423
  blakeana **393, 423**; Pl. 4, fig. 8; Pl. 5, fig. 1
Tetraodontiformes 95
Tetrasphaera 132
Thalamocyathidae 317
Thalamocyathus 317, 318, 319
  flexuosus 318
  trachealis 318, 319
Thallites 219, **220–221**
  catenelloides 222*, **223–224**
  uralensis 223
  valdensis **221–222*–223**
  willsi 224
  yabei 220
  zeilleri 219
Thallophyta 210, 211, 214
Thamnograptus 185
Thecidea 40
  papillata 11, **40**, 41, **42**; Pl. 1, figs. 9, 10
Thrissops 84, 85
Thyracella 26
  cf. *meudonensis* **26**, 41; Pl. 2, figs. 4–6
Tomocyathus **334**, 340, 369, 372
  (Erugatocyathus) 299, **334**, 372
  compositus 334
  echinus 334
  gini 334
  kundatus 334
  papillatus **334–335*–336**; Pl. 11, fig. 2
  shoriensis 334
  (*Tomocyathus*) *michniaki* 334
  operosus 334
Tortula 218
Trachichthyidae 67, 68, **69**, 77, 94, 95, 96
Trachichthyoides ornatus 78
Trachichthys 68
Trachinocephalus 81
Trachycythere **428**
  verrucosa 428
  sp. **428**; Pl. 16, fig. 3
Trachyleberididae 394, 401, 428
Trachyleberidinae 401
Trichodinium **131**, 132, 162
  castaneum **131–132**; Pl. 11, figs. 1, 2, 3
  intermedium 132
  paucispinum 163
Trichodium castanea 131
Triletes 224
Truncatula tetrasticha 17
Truncatula truncata 17
Tselfatiidae 98
Tubantia **74**
  cataphractus 74*
Tumuliolynthus 302, **304**, 369
  irregularis **304–305**; Pl. 1, fig. 1
  karakolensis 304
  musatovi 304
  tubexternus 304
  vologdini 304
Tumulocoscininae **338**
Tumulocoscinus 338
Tunkia 302
Tuvacyathus 325

Unio karooensis 259

BRITISH MUSEUM
11 SEP 1970
NATURAL HISTORY

Velifer 81, 97
Veliferidae 78, 98
Velumella 27
Vincularia **27**, 28
  canalifera **27–28**, 41; Pl. 5, figs. 7–10; Pl. 8, figs. 9–12
  concinna 28; Pl. 8, fig. 13
  flexuosa 27, 28; Pl. 8, fig. 14
  fragilis 27
  rugica 32
  transversa 32
  undata 32
Volvacyathus 354, 356, 370
Vomer 98
Vomeridae 98
Vomeropsis 98

Weichselia 236, 239
  mantelli 236, 239
  reticulata 236, **239**; Pl. 6, fig. 5
Wetlugosaurus 291
Wilbertopora mutabilis 13
Worthenopora 13, 14
Worthenoporidae 13

Xanthidium ramosum 172
  spinosum 166
  tubiferum 143
  complex 146
Xenichthys 87
Xenistitius 87
Xenocys 87
Xenolepidichthys 96

Zambiasaurus 257, 259, **260–261**, 281, 282, 283, 284, 287, 290, 292
  submersus 257, 262–263*–264*–265–266*–267–268*–269*–270*–271*–272*–273*–274*–275*–276*–277*–278*–279*–280*–281*–282*–286
Zeidae 96
Zeiformes 49, 93, 96, 97, 100
Zeus 96
Zonacyathus **314–315**, 369
  flexum 369
  poletaevae 369
  retevallum 314, **315–316**, 317, Pl. 4, figs. 4, 5
  retezona 315, **316*–317**; Pl. 4, figs. 1–3
  vermiculatum 369
Zone of *Climacograptus wilsoni* 189, 190, 195
  Dicranograptus clingani 185, 188, 192, 193, 195
  Didymograptus extensus 195
  Monograptus convolutus 196
  Monograptus cyphus 193
  Monograptus gregarius 196
  Monograptus riccartonensis 203
  Monograptus sedgwickii 196
  Orthograptus vesiculosus 193
  Pleurograptus linearis 185, 188, 192, 193, 195

PRINTED IN GREAT BRITAIN
BY ADLARD & SON LIMITED
BARTHOLOMEW PRESS, DORKING